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PEATMOSES OF THE SOUTHEASTERN STATES

By H. L. BLOMQUIST

PLATES 1 5

The peatmosses, or what are botanically known as species of *Sphagnum*, comprise a unique group of plants with more than usual botanical interest. They are commonly classed with the mosses although their structure is quite unlike that of a typical moss.

Aside from their interest to the botanist, they are also of some economic importance. Not being subject to ordinary decay, the dead parts accumulate, especially in colder climates, in deep and extensive deposits. These deposits, which are familiar to everyone as peat, serve in some parts of the world as an important source of fuel. Besides their resistance to decay, due to their antiseptic property, they also have the quality of absorbing and holding large quantities of water. The combination of these two qualities makes them of value in dressing wounds and they have been used for this purpose to some extent, especially in times of war. For the same reason they are often used in packing live plants during transportation. Also in recent years there has been a growing practice of mixing groundup peat with soil to increase the water-holding capacity of the latter.

In view of the fact that peatmosses are interesting and to a certain extent important plants, it is rather surprising how few people in this country have made an attempt to learn to distinguish the different kinds. After devoting some effort to the identification especially of those species occurring in the southeastern states, the author has come to the conclusion that this apparent lack of interest is partly due to the fact that the peatmosses have a traditional reputation of being extremely difficult to identify and partly to the lack of illustrated keys by means of which the characters could be better understood.

The purpose of this paper is, therefore, to present an illustrated key to the peatmosses of the southeastern states with the hope that it will stimulate interest and effort in learning to recognize the different kinds.

In the identification of plants it is of fundamental importance that one has correct notions of the characters referred to in the keys and descriptions. It is also important to have a knowledge of the range of variation exhibited by the characters concerned in order to appreciate their relative taxonomic values. Such facts are acquired only through a morphological study of the plants, including their developmental history. This is especially necessary in a highly specialized group such as *Sphagnum* which is given little or no attention in the general courses in botany and even to a limited extent in the more advanced courses in comparative morphology. It has, therefore, seemed desirable to review in some detail the principal structural features of sphagnum with the hope that by referring to the illustrations the characters can be more easily visualized.

#### STRUCTURAL CHARACTERISTICS OF SPHAGNUM

As in other mosses, sphagnum has a stem and leaves. In cross section the stem shows two principal regions, a cortex and a central axis (fig. 3). The cortex is composed of one to five layers of hyaline-cells which may (fig. 2) or may not (fig. 45) have fibril-bands and pores similar to those found in the leaves. There is also considerable variation in the size and shape of these cells and the thickness of their walls (figs. 48, 74).

Occasionally the stem forks into two uniform branches (dichotomy), and, as these branches grow indefinitely, they are said to be of unlimited growth (fig. 1). Besides this mode of branching, the stem bears fascicles of branches which are of limited growth. These branches are of two kinds, the spreading or divergent and the slender, drooping (fig. 1). At the summit of the stem the branches are short and crowded forming a tuft called the *capitulum*. The structure of these branches is in general like that of the stem, i.e. with a cortex and a central axis. The cortex of these branches is, however, made up of only one layer of hyaline-cells (fig. 13) which may be uniform (fig. 2) or differentiated into two kinds, large "retort-cells" and smaller cells without pores (fig. 83).

The leaves are composed throughout of one layer of cells in thickness. The cells are of two kinds, large clear or hyaline-cells, devoid of contents except for air or water, and smaller green or chlorophyllose-cells. These two kinds of cells alternate in such a way that the chlorophyllose-cells form a complete network with the hyaline-cells in the meshes (fig. 14).

The hyaline-cells are somewhat cylindrical in cross section and are, at least in the branch-leaves (except in *S. macrophyllum*), provided on the

inside with narrow ring-like or spiral ridges (fibrils) and with pores in the convex free walls (fig. 6) and to some extent between the cells. The margin of these pores may be thin or distinctly thickened. Occasionally the hyaline-cells are divided (fig. 36). Except for the fibril-bands they are commonly smooth on the inside. In some species, however, that part of the wall adjacent to the chlorophyllose-cells is covered with papillae (fig. 34) or ridges (fig. 58).

While there is considerable variation among different species in the arrangement of the fibril-bands, they are of little or no practical taxonomic value. The pores, on the other hand, which vary in number, size, shape, and position in the different species, are often referred to in keys and descriptions (see illustrations).

Besides the regular pores referred to above, there are sometimes irregular openings in the walls of the hyaline cells in the form of eroded gaps which are called "resorbed" areas. These are conspicuous on the outer walls of the cells at and near the apex of the branch-leaves in the species of the subgenus *Inophloea* (fig. 5), as well as in the stem-leaves of this and certain other groups (fig. 35). In some species the hyaline-cells are resorbed on both sides in the stem-leaves, leaving the chlorophyllose-cells loose and, therefore, forming a more or less lacerate leaf (fig. 95).

The chlorophyllose-cells, which are long and narrow, vary considerably in shape in cross section. They may be lenticular, rectangular, trapezoidal, or triangular (see illustrations). They are fairly constant, however, in the different groups, and, therefore, serve as an important taxonomic character.

The relation between the hyaline-cells and the chlorophyllose-cells is likewise of taxonomic importance. This relation is concerned first of all with the location and exposure of the chlorophyllose-cells. In some species they are more or less centrally located between and completely included by the convex walls of the adjacent hyaline-cells (figs. 21, 25). In other species the hyaline-cells include the chlorophyllose-cells on one side only so that the inner or outer walls of the latter are exposed (fig. 59). In still others the chlorophyllose-cells are exposed on both surfaces (fig. 46). Another phase of this relation, which is related to the comparative size of the two kinds of cells, is the extent to which the free convex walls of the hyaline-cells bulge out beyond the chlorophyllose-cells (compare fig. 12 with fig. 89).

Another feature of importance in the leaves concerns the lateral margins. The margin may be composed of a single row of chlorophyl-



lose-cells bordered on the outer edge by a narrow strip of an incomplete hyaline-cell. This narrow strip is known as the "resorption furrow" (figs. 10, 11). In other forms, however, this resorption furrow is absent and the margin is composed of few to several rows of narrow, elongated cells (fig. 75).

In most species of sphagnum there are several types of leaves. The two main types are, of course, the branch- and stem-leaves (figs. 4, 8). The branch-leaves are closely imbricated while the stem-leaves are usually some distance apart. They are commonly quite unlike in size, shape, and structure (*dimorphic*). In exceptional cases, however, as in *S. cyclophyllum* and *S. Pylasii*, the leaves on the stem and branches are regularly quite uniform (*isophyllous*). Isophylly may occasionally appear in varying degrees in almost any species, but it is more common in some than in others. A tendency toward this condition is known as *hemi-isophylly*.

Other types of leaves are those which subtend or surround the reproductive organs, the antheridia and archegonia. In the case of the antheridia (*perigonial-leaves*), these leaves are not essentially different from the ordinary branch-leaves except occasionally they are more deeply pigmented. The *perichaetial-leaves*, i.e., those surrounding the archegonia, are, on the other hand, quite unlike the other leaves.

The antheridia are borne in the axils of the perigonial-leaves on special branches at the base of the capitulum. When these branches are highly colored, which is often the case, they are quite conspicuous and, hence, easily located. The archegonia are borne at the tip of short branches near the center of the capitulum and in order to find them it is necessary first to locate the perichaetial-leaves which are usually larger than the other branch-leaves. Sphagnum may be either monoecious or dioecious.

After fertilization and the consequent development of the sporophyte, the tip of the archegonial branch elongates forming a naked stalk or false seta (*pseudopodium*) which elevates the capsule above the perichaetial-leaves. Unlike the true mosses, the capsules and spores in sphagnum are of little or no taxonomic significance. This is rather fortunate as the plants are not often in fruit when collected.

#### SYSTEMATICS

Taxonomically the peatmosses have been a difficult group to the botanists. This is due in part to the fact that the characters upon which the keys and descriptions are based are mostly microscopic and somewhat difficult to recognize. Sphagnum is, however, not unique in this

respect as many other plant groups are distinguished by equally obscure characters which, in order to see and understand them, require considerable experience.

The real difficulty of identification, however, has been due to the enormous variation exhibited by the plants themselves and to the selection of some characters for the delimitation of species which intergrade too much to be of any value. This has led to much general confusion and disagreement among students of peatmosses. Opinion has varied from the one extreme of placing all forms of sphagnum into one species to the other extreme of making a large number of species and many varieties. Concerning the questions of phylogeny there has also been considerable disagreement.

So far as the North American species are concerned—and these include the majority of the peatmosses of the world—much of the confusion in taxonomy and phylogeny has been cleared up in the classical treatment by A. LeRoy Andrews.<sup>1</sup> With a conservative viewpoint and a broad concept of species, Andrews has, after a careful study of a wide range of material, reduced a large number of species to synonymy and limited the varieties to only a few.

In the study of peatmosses it has long been recognized that they fall naturally into groups and subgroups. This has been discussed fully by Andrews in a series of papers entitled "Notes on the North American Sphagnum."<sup>2</sup> The characters upon which these subdivisions are based will be briefly reviewed.

Following the concepts and terms of Russow,<sup>3</sup> Andrews divides the species of *Sphagnum* into two groups: I. *Inophloea* (fibrillose cortex) and II. *Litophloea* (smooth or non-fibrillose cortex). These categories are considered as subgenera and, since the two groups are sharply distinct, the suggestion is made that they might ultimately be elevated to generic rank.

#### SUBGENUS INOPHLOEA

The most conspicuous character of the subgenus *Inophloea* is the presence of spiral-fibrils in the cortical-cells of the stem and branches and the uniformity of these cells (fig. 2). Other characters correlated with this one are: (1) the cucullate apex of the branch-leaves in which the outer surface is roughened due to the erosion ("resorption") of the

<sup>1</sup> North American Flora 15, Pt. 1: 1-31. 1913.

<sup>2</sup> The Bryologist 14: 72-75, 1911; 15: 1-7, 70-74, 1912; 16: 20-24, 59-62, 74-76, 1913; 18: 1-6, 1915; 20: 84-89, 1917; 22: 45-49, 1919; 24: 81-86, 1921.

<sup>3</sup> Zur Anatomie der Torfmoose, p. 27 f., Dorpat, 1887.

outer walls of the hyaline-cells (figs. 4, 5); (2) the undifferentiated leaf margin with the presence of a resorption furrow (figs. 10, 11); (3) a uniform narrowing of the hyaline-cells at the base of the stem-leaves; (4) the transformation of the hyaline-cells of the perichaetial-leaves into uniformly long, narrow cells only in the basal and middle portion of the leaf; and (5) the resorption of the outer wall of the hyaline-cells of the stem leaves (figs. 9, 35), although this character is not confined exclusively to this group.

All of the species of this subgenus found in North America are represented in our area.

#### SUBGENUS LITOPHLOEA

In contrast to *Inophloea*, the second subgenus *Litophloea* is characterized by the absence of spiral-fibrils in the cortical-cells. Other characters correlated with these are: (1) apex of branch-leaves straight or only slightly cucullate, usually toothed and smooth on the back (figs. 40, 41); (2) leaf margin highly differentiated, consisting of several rows of narrow, elongated cells (fig. 75); (3) a tendency to suppression of the hyaline-cells in the basal region of the stem-leaves together with a differentiation of a distinct border of several rows of narrow cells (fig. 82); and (4) the transformation of the hyaline-cells in the perichaetial-leaves into uniformly long and narrow cells in the basal, lateral, and apical regions. The resorption of the hyaline-cell walls of the stem-leaves alternates from the outer to the inner side in the different groups.

*Litophloea* is the larger of the two subgenera. Since most of the species which comprise it have northern affinities it is not as well represented in the southeastern states as *Inophloea*.

The species of the subgenus *Litophloea* fall naturally into several groups and subgroups, and Andrews has adopted the following classification:

#### SECTION MALACOSPHAGNUM

This is considered as a transition group between the *Inophloea* and *Litophloea* since the species comprising it show some resemblances to both subgenera. The cortical-cells are without fibrils but are all of the retort type (fig. 22), which distinguishes this section from the other sections of the subgenus. The margin of the branch-leaves shows a resorption furrow as in *Inophloea*, but the stem-leaves have a differentiated border typical of *Litophloea*.

The two species found in North America which belong to the section *Malacosphagnum* occur in our area.

## SECTION ACISPAGNUM

The characters common to the species of this section are more typical of the subgenus *Litophloea*. The section has been divided into the following "groups:" *Squarrosa*, *Cuspidata*, *Acutifolia*. These groups are separated mainly on the basis of the location of the resorption gaps in the hyaline-cells of the stem- and perichaetial-leaves.

In the *Squarrosa* group, the outer membrane of the hyaline-cells of both stem- and perichaetial-leaves is resorbed as in *Inophloea*, while in the other two groups resorption occurs on the inner side of the stem-leaves. In the *Cuspidata* group, resorption takes place on the inner side of the perichaetial-leaves but is entirely absent in the *Acutifolia*. In some species of the *Cuspidata* and *Acutifolia* groups resorption may take place to a certain extent on both surfaces of the stem-leaves, giving the leaf a conspicuously lacerate appearance which, being easily observed, is a convenient diagnostic character. Other practical diagnostic characters of these groups are, the shape and exposure of the chlorophyllose-cells of branch-leaves, the character of the cortical-cells of the stem, and the size and shape of the stem-leaves. Furthermore the pigment of the *Cuspidata* group is brown, while that of the *Acutifolia* group is usually red. The practical value of this character is questionable, however, since there is considerable variation in the degree of pigmentation even to the extent that it may be absent altogether.

As the *Squarrosa* group is typically northern in its distribution, it barely reaches the southeastern states. The only species present is *S. squarrosus* which reaches its southern limit in western North Carolina and eastern Tennessee.

The *Cuspidata* group, on the other hand, is well represented with seven species, some of which, such as *S. Fitzgeraldi*, *S. macrophyllum* and *S. cyclophyllum*, are more or less southern in their distribution.

Although the *Acutifolia* group may in general be said to be composed largely of northern peatmosses, it is represented in the southeastern states by six species. One of these, *S. meridense*, is exclusively tropical.

In the consideration of phylogeny in *Sphagnum*, as in other plants, the relative position of the various categories is determined by the degree of differentiation or specialization. Uniformity of cell structure should, therefore, indicate a primitive position. This is illustrated by the subgenus *Inophloea* in which the cortical cells of the branches are not only uniform but are, like the hyaline-cells of the branch-leaves, also provided with spiral-fibrils. Correlated with this uniformity is the low degree of differentiation of the leaf margin. *Litophloea*, on the

other hand, shows a higher degree of differentiation in the absence of fibrils from the cortical-cells, and especially in the fact that two kinds of cells are present in the cortex of the branches. These characters, together with a highly differentiated leaf margin, place this group higher in the scale of evolution than *Inophloea*.

The included chlorophyllose-cell (fig. 21) is a primitive character but, since this occurs in the various groups, it cannot be considered of major phylogenetic importance.

According to the above concepts and interpretation of facts, the classification of the species of *Sphagnum* which have been found to occur in the southeastern states may be outlined as follows:

- Subgenus I. *Inophloea*
  - S. magellanicum*
  - S. papillosum*
  - S. erythrocalyx*
  - S. palustre*
  - S. henryense*
  - S. imbricatum*
  - S. portoricense*
- Subgenus II. *Litophloea*
  - Section I. *Malacosphagnum*
    - S. compactum*
    - S. strictum*
  - Section II. *Acisphagnum*
    - Group a. *Squarrosa*
      - S. squarrosum*
    - Group b. *Cuspidata*
      - S. recurvum*
      - S. cuspidatum*
      - S. Fitzgeraldi*
      - S. subsecundum*
      - S. Pylaesii*
      - S. cyclophyllum*
      - S. macrophyllum*
    - Group c. *Acutifolia*
      - S. Girgensohnii*
      - S. capillaceum*
      - S. quinquefarium*
      - S. meridense*
      - S. tenerum*
      - S. tabulare*

The specimens upon which this report is based are mainly the collections in the Duke University Herbarium from North and South Carolina,

Georgia, Florida, Alabama, Mississippi, and eastern Tennessee. The key may no doubt be used, however, in the other states south of the Mason Dixon Line east of the Mississippi River.

#### TECHNIQUE

In the use of the following key it might be helpful to add a few remarks concerning the technique in making the necessary analysis.

For the examination of most details, the material should be moist. The cortical-cells of the branches may be examined after the removal of the leaves by means of a scalpel or a needle. In examining the stem or the stem-leaves, the fascicles of branches should be removed from the stem. The cortex and leaves may be viewed from the surface but, due to the opaqueness of the central region, it is best to scrape off some of the cortex and leaves. To determine the number of layers of cortical-cells it is necessary to make a thin section of the stem with a sharp scalpel or razor blade under a binocular microscope or in pith.

In the examination of leaves it is necessary to select a *typical* leaf. This is not difficult in stem-leaves except in hemi-isophyllous forms. The branch-leaves vary considerably from base to apex and it is, therefore, best to select a leaf from the plumpest part of the branch which is usually about its middle portion. The sectioning of leaves may be done freehand under a binocular or in pith. In slender forms with small leaves, satisfactory sections can usually be obtained by sectioning the branch with the leaves intact. In more robust forms individual leaves may be sectioned successfully. The advantage of sectioning an individual leaf is that the desired (median) section can then be obtained at will instead of by chance. The purpose of sectioning leaves is to obtain a view of the shape of the cells, especially the chlorophyllose-cells, and to determine the position of the resorption gaps. With some experience a considerable amount of sectioning may be dispensed with as one soon learns to interpret the shape and exposure of cells and the presence and position of resorption gaps from surface views (consult the illustrations). In order that certain features, such as pores and resorbed areas, can be more easily observed, it is often advantageous to use dyes, such as methylene blue, safranin, or gentian violet. In examining the hyaline leaf cells for pores, it should be borne in mind that these vary to a great extent throughout the leaf and that reference is usually made to the cells in the middle of the leaf.

KEY TO SPECIES AND VARIETIES<sup>4</sup>

- 1a. Cortical-cells of the stem and branches uniform with fibril-bands (2)\*; apex of branch leaves cucullate (4) with the outer hyaline-cells conspicuously eroded (5); resorption furrow present (10, 11).
  - 2a. Chlorophyllose-cells of branch-leaves entirely included (25) or exposed about equally on both surfaces of the leaf (20, 34), narrowly rectangular to lenticular in section.
    - 3a. Chlorophyllose-cells entirely included, half way between both surfaces, short-lenticular in section (25).....1. *S. magellanicum*
    - 3b. Chlorophyllose-cells exposed about equally on both surfaces, narrowly rectangular to lenticular in section.
      - 4a. That part of the wall of the hyaline-cells adjacent to the chlorophyllose-cells papillose (34); chlorophyllose-cells truncately elliptic in section (34).....2. *S. papillosum*
      - 4b. That part of the wall of the hyaline cells adjacent to the chlorophyllose-cells not papillose; chlorophyllose-cells narrowly rectangular in section (20).....3. *S. erythrocalyx*
  - 2b. Chlorophyllose-cells of branch-leaves exposed more broadly on the inner surface of the leaf, triangular to rounded-triangular in section (12, 59).
    - 5a. Chlorophyllose-cells of the branch-leaves isosceles-triangular in section; walls of median hyaline-cells with few or no pores on the inner side of the leaf (7, 16).
      - 6a. That part of the wall of the hyaline-cells of branch-leaves adjacent to chlorophyllose-cells smooth  
4. *S. palustre*
      - 6b. That part of the wall of the hyaline-cells of the branch-leaves adjacent to chlorophyllose-cells with an irregular network of longitudinal ridges (15), especially at the base of the leaf...5. *S. henryense*
    - 5b. Chlorophyllose-cells of branch-leaves equilateral-triangular in section (31); the median hyaline-cells with several pores on the inner side of the leaf (57).
      - 7a. Cortical-cells of the branches with the end-walls straight (2), not funnel-shaped.
        - 8a. That part of the wall of the hyaline-cells of the branch-leaves adjacent to the chlorophyllose-cells with conspicuous comb-like ridges (58), especially at the base of the leaf.....6. *S. imbricatum*
        - 8b. That part of the wall of the hyaline-cells of the branch-leaves adjacent to the chlorophyllose-cells without ridges  
6a. *S. imbricatum* v. *affine*
      - 7b. Cortical-cells of the branches with funnel-shaped ends (30).....7. *S. portoricensis*
  - 1b. Cortical-cells of the stem and branches without fibril-bands, those of the branches uniform (22) or of two kinds (45, 83); apex of branch-leaves little or not at all cucullate (87, 99), usually toothed (40), hyaline-cells not eroded on the outside; resorption furrow present or absent, when absent the border consisting of a row of few narrow elongated hyaline-cells (75).

<sup>4</sup> This key has been adapted to a great extent from Andrew's key to the species of *Sphagnum* of North America (Ibid.). This as well as his *Notes on American Sphagnum* (Ibid.) should be consulted for more detailed descriptions.

<sup>5</sup> The numbers refer to the figures.

- 9a. Resorption furrow present in the branch-leaves; cortical-cells of the branches more or less uniform, each with a pore at the upper end (22).
  - 10a. Chlorophyllose-cells completely included, closer to the outer surface, elliptic in section (21)..... 8. *S. compactum*
  - 10b. Chlorophyllose-cells exposed on the outer surface, rounded-triangular in section (61)..... 9. *S. strictum*
- 9b. Resorption furrow absent (75), cortical-cells of the branches of two kinds, the large retort cells and the smaller cells without pores (83), or, if uniform, all without pores.
  - 11a. Chlorophyllose-cells of the branch-leaves triangular (68A) to trapezoidal (37) or rounded-rectangular (46), *exposed more broadly on the outer surface*.
  - 12a. Chlorophyllose-cells triangular in section and exposed on the outer surface (68A).
    - 13a. That part of the wall of the hyaline-cells of the branch-leaves adjacent to the chlorophyllose-cells papillose (68A); stem-leaves somewhat fimbriate at the broad apex; branch-leaves usually conspicuously squarrose (66)
      - 10. *S. squarrosus*
    - 13b. That part of the wall of the hyaline-cells of the branch-leaves adjacent to the chlorophyllose-cells not papillose; stem-leaves not fimbriate at the usually narrow and toothed apex (40).
    - 14a. *Branch-leaves, when dry, with spreading and usually twisted tips* (69); cortical-cells of the stem uniform, small, thick-walled and without pores (72, 74)
      - 11. *S. recurvum*
    - 14b. *Branch-leaves, when dry, not with spreading or twisted tips* (41); cortical-cells of the stem larger, thin-walled (47, 48), at least some with pores.
    - 15a. Branch-leaves lanceolate to long-lanceolate (41), *not serrulate on the margin*; plants not delicate.
    - 16a. Branch-leaves not undulate when dry; plants not always submerged aquatic
      - 12. *S. cuspidatum*
    - 16b. Branch-leaves undulate when dry; plants more robust, usually submerged
      - 12a. *S. cuspidatum* v. *Torreyi*
    - 15b. Branch-leaves mostly linear-lanceolate, *serrulate on the margin by the projecting ends of the border cells* (42), plants delicate, always aquatic..... 12b. *S. cuspidatum* v. *serrulatum*
  - 12b. Chlorophyllose-cells of branch-leaves in section from trapezoidal (37) with broader exposure on the outer surface to rectangular or rounded-rectangular with equal exposure on both surfaces (46, 56).
    - 17a. Hyaline cells of the branch-leaves without fibril-bands, long and narrow, with a single row of pores in the middle of the outer wall (54)
      - 17. *S. macrophyllum*
    - 17b. Hyaline-cells of the branch-leaves with fibril-bands, not with a single central row of pores.



- 18a. Chlorophyllose-cells in section triangular-trapezoidal with lumen triangular (37); branch-leaves not strongly concave when dry (41, 42, 60).
- 19a. Branch-leaves short- to long-lanceolate or linear-lanceolate; stem-leaves usually small, not hemi-isophyllous; plants greenish
12. *S. cuspidatum* and varieties (see above)
- 19b. Branch-leaves short-ovate to oblong or nearly quadrate (60); stem-leaves large, hemi-isophyllous; plants delicate and whitish
13. *S. Fitzgeraldi*
- 18b. Chlorophyllose-cells in section trapezoidal with broader exposure on the outer surface to rectangular or rounded-rectangular with about equal exposure on both surfaces, the lumen trapezoidal, rectangular or lenticular; branch-leaves strongly concave when dry.
- 20a. Plants with typical fascicles of branches (1); leaves ovate to ovate-lanceolate, usually not isophyllous; chlorophyllose-cells of branch-leaves rounded-rectangular to truncately elliptic in section and exposed about equally on both surfaces, or broadly trapezoidal and exposed more broadly on the outer surface.
- 21a. Chlorophyllose-cells of branch-leaves truncately elliptic in section, the lumen lenticular (84); outer walls of hyaline cells of branch-leaves with a few large pores or none, the inner walls with several large pores in different parts of the wall (85, 86); branch-leaves deeply concave, abruptly involute-acuminate (87); plants exclusively tropical . . . . . 21. *S. meridense*
- 21b. Chlorophyllose-cells of branch-leaves rounded-rectangular, exposed equally on both surfaces, to broadly trapezoidal and exposed more broadly on the outer surface; outer walls of hyaline-cells typically with numerous small, elliptic strongly ringed pores in bead-like rows along the sutures (44), at least in the upper part of the leaf, the inner walls with few or no pores (43); branch-leaves gradually involute-acuminate to acute (41); plants not exclusively tropical
14. *S. subsecundum*
- 20b. Plants without typical fascicles of branches (49, 50); leaves almost orbicular (52); isophyllous (49, 50); chlorophyllose-cells of branch-leaves rectangular in section and exposed equally on both surfaces (56).
- 22a. Plants short, sparingly branched (49, 50), plump, brown in color, growing at low altitudes; pores on the outer surface of the hyaline-cells more than 2 per cell
15. *P. cyclophyllum*
- 22b. Plants longer, more branched, slender, dark-brown to black, growing at high altitudes; pores when present not more than 2 per cell . . . . . 16. *P. Pylaesii*
- 11b. Chlorophyllose-cells of the branch-leaves triangular to trapezoidal in section, exposed more broadly on the inner surface.
- 23a. Plants without typical fascicles of branches (49, 50); color brown to black; leaves almost orbicular (52), isophyllous (49, 50); chlorophyllose-cells trapezoidal in section
- P. cyclophyllum* and *P. Pylaesii* (see above)
- 23b. Plants with typical fascicles of branches (1), color, if any, red; leaves not orbicular nor isophyllous; chlorophyllose-cells triangular to trapezoidal in section.

- 24a. Stem-leaves conspicuously fimbriate-lacerate (95) at the broad apex  
18. *S. Girgensohnii*
- 24b. Stem-leaves not fimbriate-lacerate at the apex, often toothed.
- 25a. Hyaline-cells of the branch-leaves in proportion to the chlorophyllose-cells large in section (89, 96), *their free convexity on the outer surface usually more than half their diameter*, strongly convex on the inner surface (89, 96).
- 26a. *Upper margin of the branch leaves not denticulate*; chlorophyllose-cells in proportion to the hyaline-cells very small, usually exposed on both surfaces (89); hyaline-cells strongly convex on the inner surface; plants commonly not short and stout; stem-leaves usually not hemi-isophyllous ..... 22. *S. tenerum*
- 26b. *Upper margin of the branch leaves denticulate* (99); chlorophyllose-cells not very small (96), usually exposed only on the inner surface; hyaline-cells not strongly convex on the inner surface (96); plants commonly short and stout; stem-leaves often hemi-isophyllous  
23. *S. tabulare*
- 25b. Hyaline-cells of the branch-leaves in proportion to the chlorophyllose-cells smaller in section, *their free convexity on the outer surface usually less than half their diameter* (81), little convex on the inner surface (78, 81).
- 27a. *Branch-leaves gradually involute-acuminate to acute* (88), outer surface of hyaline-cells with several large pores; plants not exclusively tropical.
- 28a. *Stem-leaves large*, lingulate to lingulate-ovate, one and one-half or more as long as wide (80); hyaline-cells with some free convexity on the inner surface.
- 29a. Stem leaves narrowly lingulate to triangular-ovate, *few or no hyaline-cells of stem-leaves divided* (14); plants not slender ..... 19. *S. capillaceum*
- 29b. Stem leaves broad-lingulate; *hyaline-cells of stem-leaves mostly divided* (36); plants commonly slender  
19a. *S. capillaceum* v. *tenellum*
- 28b. *Stem-leaves smaller, not much longer than wide*, triangular to triangular-lingulate (79); hyaline-cells with little or no free convexity on the inner surface (78)  
20. *S. quinquefarium*
- 27b. Branch-leaves *abruptly involute-acuminate* (87); outer surface of hyaline-cells with few or no pores; *plants exclusively tropical*  
21. *S. meridense*

#### ANNOTATED LIST OF SPECIES AND VARIETIES

1. *Sphagnum magellanicum* Brid. (*S. medium* Limpr., *S. intermedium* Russow.) Figs. 25, 26, 27.

Not common. Distribution general throughout the area.

Often recognized in the field by its reddish color. The only species of the subgenus *Inophloea* with included chlorophyllose-cells; the only other species with included chlorophyllose-cells is *S. compactum* from which it is easily distinguished by its fibrillose cortical-cells.

2. **Sphagnum papillosum** Lindb. Figs. 32, 33, 34.

Rare. Reaching its southern limit in the upper coastal plain of southeastern North Carolina.

Closely related to *S. erythrocalyx* from which it is easily distinguished by its papillose lateral regions of the hyaline leaf-cells and its larger pores on the outer walls of the hyaline-cells. This species has been found most suitable for surgical dressing.

3. **Sphagnum erythrocalyx** Hampe. (*S. guadalupense* Schimp., *S. ludovicianum* Warnst.) Figs. 18, 19, 20.

Common. Coastal plain throughout the area.

Very variable but recognized in the field by its compact form and reddish to brown-blackish color; readily distinguished from *S. palustre* or *S. henryense* by the small pores of the hyaline-cells of the branch-leaves.

4. **Sphagnum palustre** L. (*S. cymbifolium* Ehrh.) Figs. 1-14, 35.

Common at higher altitudes, decreasing in frequency toward the coast. Throughout the area.

This species is sometimes confused with *S. imbricatum* var. *affine* and *S. henryense*. From the former it can be distinguished by the isosceles-triangular chlorophyllose leaf-cells, from the latter by the lack of a network of ridges on the lateral sides of the hyaline leaf-cells.

5. **Sphagnum henryense** Warnst. Figs. 15-17.

Rather rare. Confined to the coastal plain throughout the area.

This species might be confused with *S. palustre* unless one is careful to look for the network of ridges on the lateral sides of the hyaline leaf-cells, and the smaller, strongly ringed pores on the outer surface.

6. **Sphagnum imbricatum** Korns. (*S. Austini* Sull.) Figs. 57-59.

Fairly common. Of general distribution throughout the area.

Most easily recognized of all species by the presence of fringe-fibrils on the lateral sides of the hyaline leaf-cells, which are often only evident at the base of the leaf. Not likely to be confused with *S. portoricense* from general appearances and from the lack of funnel-shaped cortical branch-cells characteristic of the latter.

6a. **Sphagnum imbricatum** var. **affine** (Ren. & Card.) Warnst. (*S. affine* Ren. & Card.)

Of about the same frequency and distribution as the species.

7. **Sphagnum portoricense** Hampe. (*S. Sullivantianum* Aust.) Figs. 28-31.

Not common. Confined to the coastal plain; not reported from Alabama, Mississippi, and Louisiana.

Easily recognized in the field by its usual robust form and the club-shaped branches. Most closely related to *S. imbricatum*.

8. **Sphagnum compactum** DC. (*S. rigidum* Schimp.) Figs. 21-24.

Common. Of general distribution throughout the area, although not reported west of Alabama in the Gulf States.

Recognized in the field by its short and compact form which it has, however, in common with *S. strictum* and *S. tabulare*. Not likely to be confused with *S. strictum* because of its included chlorophyllose-cells and *S. tabulare* because of the same character and, in addition, by its uniform cortical-cells of the stem.

9. **Sphagnum strictum** Sull. Figs. 61-63.

Rare in the Carolinas; more frequent southward. Coastal plain, but extending into other sections throughout the area.

10. **Sphagnum squarrosum** Crome. Figs. 66-68.

Rare. Collected in western North Carolina and eastern Tennessee where it reaches the southern limit of its range.

Easily recognized in the field by its squarrose branch-leaves, and microscopically by the papillae on the lateral sides of its hyaline leaf-cells.

11. **Sphagnum recurvum** Beauv. (*S. pulchricoma* C. Mull., *S. riparioides* Warnst.) Figs. 69-75.

Fairly common. Of general distribution throughout the area.

Best recognized macroscopically in dried condition by the twisted recurved tips of the branch leaves. Quite variable and often confused with *S. cuspidatum* from which it is best distinguished by the characters given in the key.

12. **Sphagnum cuspidatum** Ehrh. (*S. virginianum* Warnst., *S. Faxonii* Warnst.) Figs. 37-41, 47.

Fairly common but decreasing southward. Coastal plain, extending into the lower piedmont; not collected west of Georgia in the Gulf States.

Growing in wet places or in water. Highly variable, grading into the following two varieties.

- 12a. **Sphagnum cuspidatum** var. **Torreyi** (Sull.) Braithw.

Rare. Not collected south of North Carolina.

This resembles to some extent *S. recurvum* in its undulate leaves but typically does not show the twisted or recurved leaf-tips.

12b. **Sphagnum cuspidatum** var. **serrulatum** Schlieph. Fig. 42.

Not common except locally. Near the coast throughout the area.

Very delicate and always growing in water. Easily recognized by the serrulate linear branch-leaves.

13. **Sphagnum Fitzgeraldi** Ren. (*S. Mohrianum* Warnst.) Figs. 60, 64, 65.

Not common. Near the coast from southeastern North Carolina to Florida and Alabama.

Recognized in the field by its delicate whitish appearance; resembling somewhat *S. cuspidatum* var. *serrulatum* but distinguished from it by the ovate to rectangular leaves which are not serrulate on the margin.

14. **Sphagnum subsecundum** Nees. (*S. auriculatum* Schimp., *S. laricinum* Spruce, *S. mobile* Warnst., *S. orlandense* Warnst., *S. inundatum* Russow., *S. Louisianae* Warnst., etc.) Figs. 43, 46, 48.

Common. Distribution general throughout the area.

This species is extremely variable as is apparent from the extensive synonymy. When typical it is easily recognized by the numerous bead-like pores along the commissures of the hyaline leaf-cells; when these are absent, the shape and exposure of the chlorophyllose-cells and the large cortical-cells of the stem will be sufficient to determine its identity.

15. **Sphagnum Pylaeii** Brid.

Rare. Found only at high altitudes in eastern Tennessee and western South Carolina where it reaches its southern limit of distribution.

This species is closely related to *S. cyclophyllum*, with which it can hardly be confused because of their differences in distribution.

16. **Sphagnum cyclophyllum** Sull. & Lesq. (*S. alabamiae* Warnst.) Figs. 51-53.

Not common. Confined to the coastal plain throughout the area.

Easily recognized in the field by its sparsity of branches and the isophyllous almost orbicular leaves.

17. **Sphagnum macrophyllum** Bernh. (*S. floridanum* Card.) Figs. 54-56.

Not common. In the coastal plain throughout the area.

This peculiar species is easily recognized—if recognized as a peatmoss—by its aquatic habitat and its general appearance.

18. **Sphagnum Girgensohnii** Russow. (*S. strictum* Lindb.) Figs. 90-95.

Rare and only at high altitudes. Collected in western North Carolina and eastern Tennessee where it reaches its southern limit of distribution in eastern North America.

In general appearance this species resembles *S. capillaceum* and *S. quinquefarium* and can best be distinguished from these two by the lacerate apex of the stem leaves.

19. **Sphagnum capillaceum** (Weiss.) Schrank. (*S. acutifolium* Ehrh.) Figs. 80-83, 88.

Common. Distribution general throughout the area but less common near the coast.

This is a highly variable species. It is easily confused with *S. quinquefarium* and *S. tenerum*, from which it can best be separated by the characters given in the key.

- 19a. **Sphagnum capillaceum** var. **tenellum** (Schimp.) A. L. Andrews. (*S. rubellum* Wilson, *S. acutifolium tenellum* Schimp.) Fig. 36.

Not common. At the higher altitudes as far south as western South Carolina.

Usually more slender and with more pigmentation than the species.

20. **Sphagnum quinquefarium** (Lindb.) Warnst. (*S. acutifolium quinquefarium* Lind.) Figs. 76-79.

Not common. Found only at higher altitudes as far south as Georgia.

Distinguished in the field sometimes by the sharply five-angled branches.

21. **Sphagnum meridense** (Hampe) C. Mull. (*S. acutifolium meridense* Hampe.) Figs. 84-87.

This is a tropical species which reaches the extreme southern tip of Florida.

Easily distinguished from the others of the *Acutifolia* group by the scarcity of pores on the outer surface of the hyaline-cells of the branch-leaves.

22. **Sphagnum tenerum** Sull. & Lesq. Fig. 89.

Rare. Collected at higher altitudes as far south as Alabama.

This species is closely related to *S. capillaceum* from which it can best be separated by its large hyaline-cells, strongly convex on both surfaces, and its minute chlorophyllose-cells.

23. **Sphagnum tabulare** Sull. (*S. molle* Sull.) Figs. 96-99.

Fairly common. From the mountains to the coast.

Sometimes recognized in the field by its compact form, its sparsity of branching and by its hemi-isophyllous or isophyllous leaves.

The writer is greatly indebted to A. LeRoy Andrews for help and encouragement in the study of sphagnum. To D. S. Correll he owes grateful acknowledgment for the majority of the specimens upon which this paper is based. In the preparation of the manuscript, Lewis E. Anderson has been of invaluable assistance in his criticisms and helpful suggestions.

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#### EXPLANATION OF PLATES

All figures except 1, 49, 50, and 55, were drawn with the aid of an Abbe camera lucida. All sections of leaves have been drawn with the inner side up.

##### PLATE 1

##### 1-14. *Sphagnum palustre*

1. Habit of plant,  $\times 1$ .
2. Surface view of cortical-cells,  $\times 44$ .
3. Transverse section of stem,  $\times 44$ .
4. Branch-leaf,  $\times 22$ .
5. Apex of branch-leaf,  $\times 235$ .
6. Outer side of cells of branch-leaf,  $\times 235$ .
7. Inner side of cells of branch-leaf,  $\times 235$ .
8. Stem-leaf,  $\times 22$ .
9. Cells in section of stem-leaf,  $\times 235$ .
10. Cells in section of edge of branch-leaf,  $\times 235$ .
11. Surface view of edge of branch-leaf,  $\times 235$ .
12. Cells in section of branch-leaf,  $\times 235$ .
13. Transverse section of branch,  $\times 44$ .
14. Surface view of cells of branch leaf,  $\times 235$ .

##### 15-17. *Sphagnum henryense*

15. Outer side of cells of branch-leaf,  $\times 235$ .
16. Inner side of cells of branch-leaf,  $\times 235$ .
17. Cells in section of branch-leaf,  $\times 235$ .

##### PLATE 2

##### 18-20. *Sphagnum erythrocalyx*

18. Inner side of cells of branch-leaf,  $\times 235$ .
19. Outer side of cells of branch-leaf,  $\times 235$ .
20. Cells in section of branch-leaf,  $\times 235$ .

21-24. *Sphagnum compactum*

- 21. Cells in section of branch-leaf,  $\times 235$ .
- 22. Surface view of cortex of branch,  $\times 44$ .
- 23. Outer side of cells of branch-leaf,  $\times 235$ .
- 24. Inner side of cell of branch-leaf,  $\times 235$ .

25-27. *Sphagnum magellanicum*

- 25. Cells in section of branch-leaf,  $\times 235$ .
- 26. Inner side of cell of branch-leaf,  $\times 235$ .
- 27. Outer side of cell of branch-leaf,  $\times 235$ .

28-31. *Sphagnum portoricense*

- 28. Outer side of cell of branch-leaf,  $\times 235$ .
- 29. Inner side of cell of branch-leaf,  $\times 235$ .
- 30. Surface view of cortex of branch,  $\times 235$ .
- 31. Cells in section of branch leaf,  $\times 235$ .

32-34. *Sphagnum papillosum*

- 32. Inner side of cells in branch-leaf,  $\times 235$ .
- 33. Outer side of cells in branch-leaf,  $\times 235$ .
- 34. Cells in section of branch-leaf,  $\times 235$ .

- 35. Resorption gaps on outer side of stem-leaf in *S. palustre*,  $\times 235$ .
- 36. Divided hyaline-cells in stem-leaf of *S. capillaceum* v. *tenellum*,  $\times 235$ .

## PLATE 3

37-41. *Sphagnum cuspidatum*

- 37. Cells in section of branch-leaf,  $\times 235$ .
- 38. Inner side of cells of branch-leaf,  $\times 235$ .
- 39. Outer side of cells of branch-leaf,  $\times 235$ .
- 40. Apex of branch-leaf,  $\times 44$ .
- 41. Branch-leaf,  $\times 22$ .
- 42. Tip of branch-leaf of *S. cuspidatum* v. *serrulatum*,  $\times 64$ .

43-46. *Sphagnum subsecundum*

- 43. Inner side of cells in branch-leaf,  $\times 235$ .
- 44. Outer side of cells in branch-leaf,  $\times 235$ .
- 45. Surface view of cortex of branch,  $\times 44$ .
- 46. Cells in section of branch-leaf,  $\times 235$ .
- 47. Section of outer region of stem of *S. cuspidatum*,  $\times 235$ .
- 48. Section of outer region of stem of *S. subsecundum*,  $\times 235$ .

49-53A. *Sphagnum cyclophyllum*

- 49, 50. Habit of plants,  $\times 2$ .
- 51. Cells in section of branch-leaf,  $\times 235$ .



52. Branch-leaf,  $\times 44$ .

53. Inner side of cells of branch-leaf,  $\times 235$ .

53A. Outer side of cells of branch-leaf,  $\times 235$ .

54-56. *Sphagnum macrophyllum*

54. Outer side of cells of branch-leaf,  $\times 235$ .

55. Habit of plant,  $\times 1$ .

56. Cells in section of branch-leaf,  $\times 235$ .

PLATE 4

57-59. *Sphagnum imbricatum*

57. Inner side of cells of branch-leaf,  $\times 235$ .

58. Outer side of cells of branch-leaf,  $\times 235$ .

59. Cells in section of branch-leaf,  $\times 235$ .

60. Upper branch-leaf of *S. Fitzgeraldi*,  $\times 44$ .

61-63. *Sphagnum strictum*

61. Cells in section of branch-leaf,  $\times 235$ .

62. Inner side of cells of branch-leaf,  $\times 235$ .

63. Outer side of cells of branch-leaf,  $\times 235$ .

64-65. *Sphagnum Fitzgeraldi*

64. Inner side of cells of branch-leaf,  $\times 235$ .

65. Outer side of cells of branch-leaf,  $\times 235$ .

66-68A. *Sphagnum squarrosum*

66. Branch leaf,  $\times 44$ .

67. Cells in section of stem-leaf,  $\times 235$ .

67A. Inner side of cells of branch-leaf,  $\times 235$ .

68. Outer side of cells of branch-leaf,  $\times 235$ .

68A. Cells in section of branch-leaf,  $\times 235$ .

69 75. *Sphagnum recurvum*

69. Branch-leaf,  $\times 44$ .

70. Inner side of cells of branch-leaf,  $\times 235$ .

71. Outer side of cells of branch-leaf,  $\times 235$ .

72. Surface view of cortex-cells of stem,  $\times 235$ .

73. Cells in section of branch-leaf,  $\times 235$ .

74. Section of outer region of stem,  $\times 235$ .

75. Surface view of border of branch-leaf,  $\times 235$ .

PLATE 5

76-79. *Sphagnum quinquefarium*

76. Outer side of cells of branch-leaf,  $\times 235$ .

77. Inner side of cells of branch-leaf,  $\times 235$ .

78. Cells in section of branch-leaf,  $\times 235$ .

79. Stem leaf,  $\times 44$ .

80-83. *Sphagnum capillaceum*

80. Stem leaf,  $\times 44$ .

81. Cells in section of branch-leaf,  $\times 235$ .

82. Lower marginal cells of stem-leaf,  $\times 235$ .

83. Cortical cells of branch,  $\times 44$ .

84-87. *Sphagnum meridense*

84. Cells in section of branch-leaf,  $\times 235$ .

85. Outer side of cells of branch-leaf,  $\times 235$ .

86. Inner side of cells of branch-leaf,  $\times 235$ .

87. Branch-leaf,  $\times 44$ .

88. Branch leaf of *S. capillaceum*,  $\times 44$ .

89. Cells in section of branch-leaf of *S. tenerum*,  $\times 235$ .

90, 93-95. *Sphagnum Girgensohni*

90. Inner side of cells of branch-leaf,  $\times 235$ .

93. Outer side of cells of branch-leaf,  $\times 235$ .

94. Cells in section of branch-leaf,  $\times 235$ .

95. Apex of stem-leaf,  $\times 44$ .

96 99. *Sphagnum tabulare*

96. Cells in section of branch-leaf,  $\times 235$ .

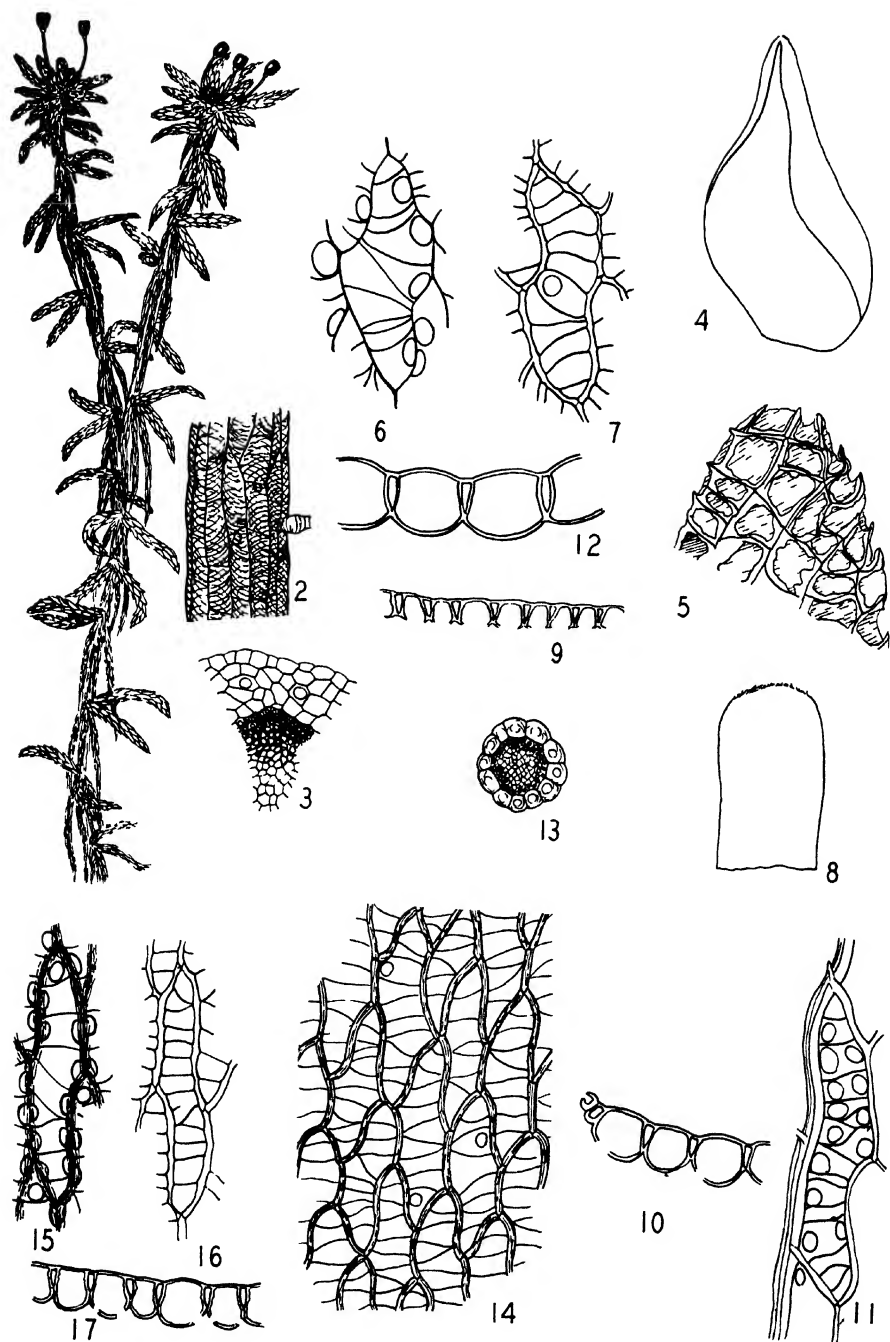
97. Outer side of cells of branch-leaf,  $\times 235$ .

98. Inner side of cells of branch-leaf,  $\times 235$ .

99. Apex of branch-leaf,  $\times 44$ .



# PLATE 1





# PLATE 2

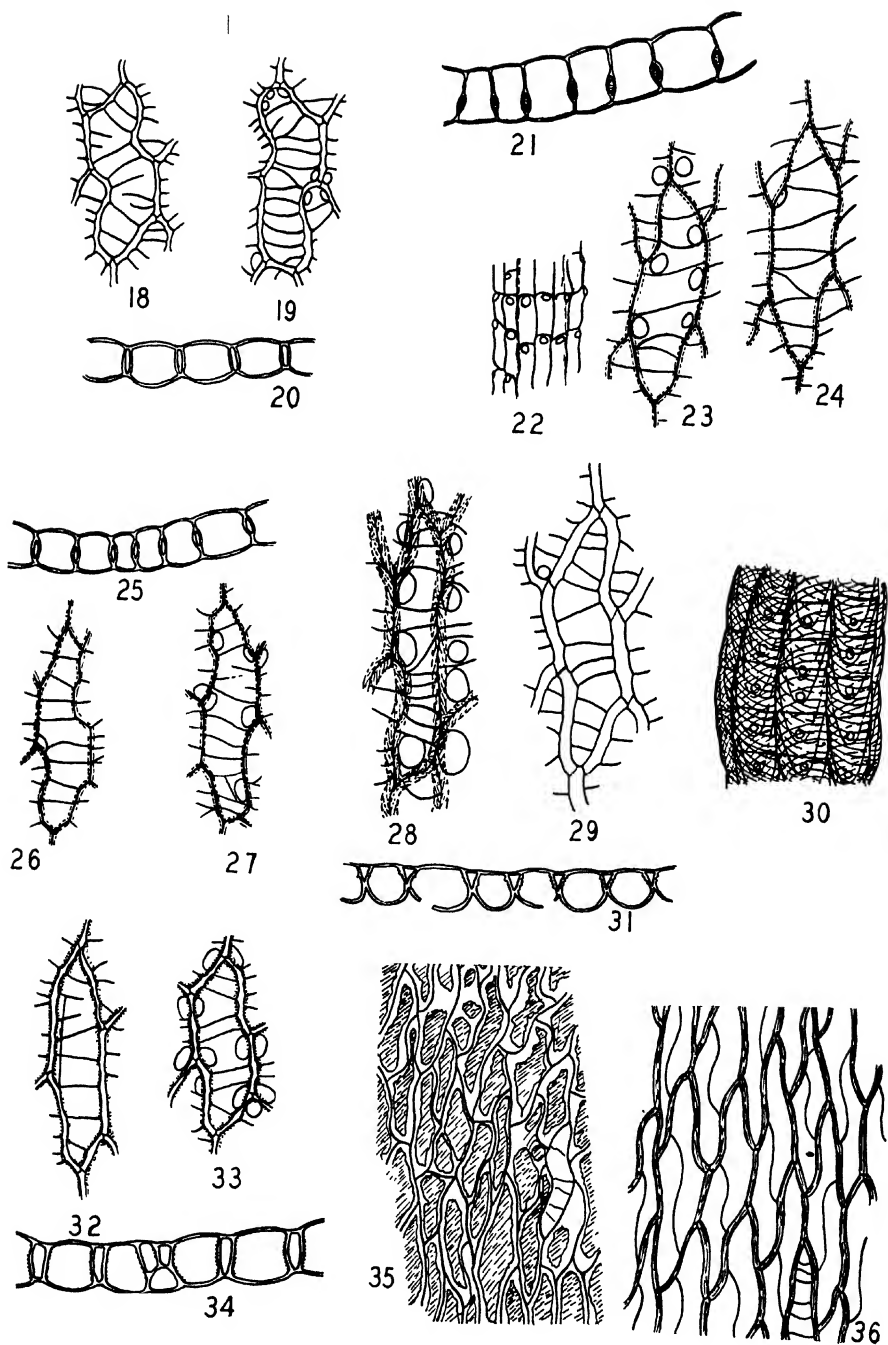




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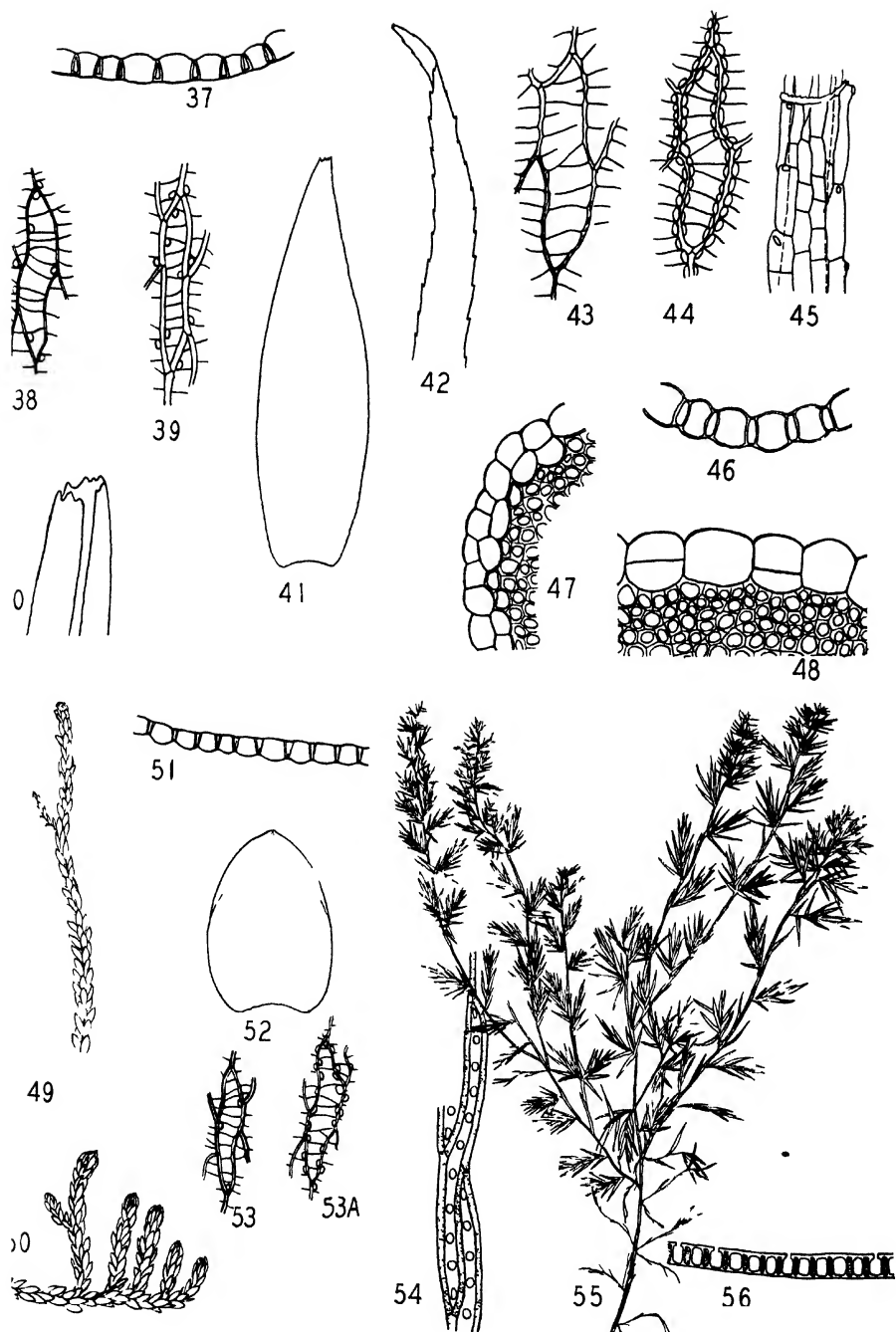






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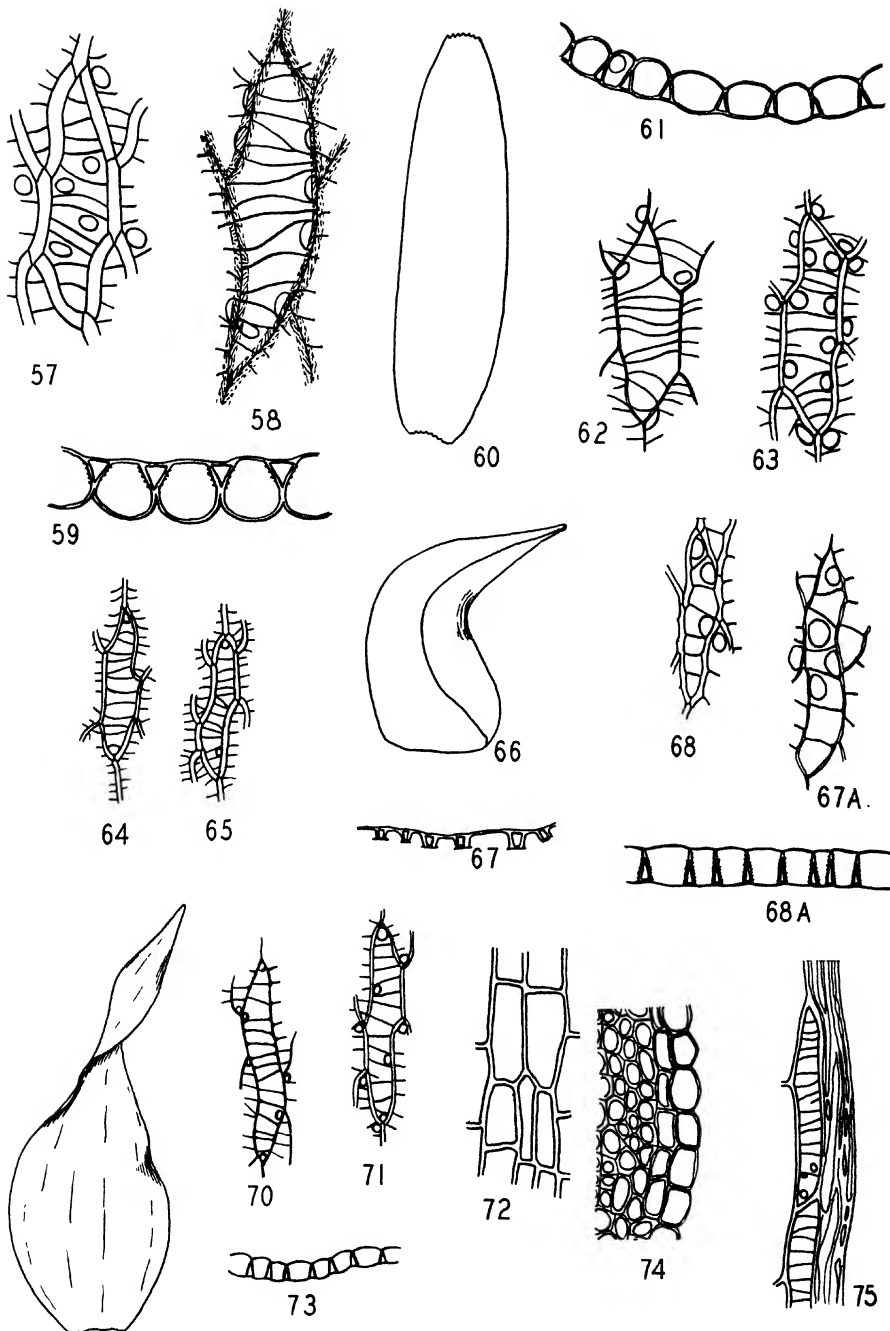
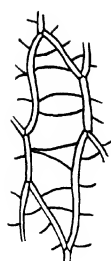




PLATE 5



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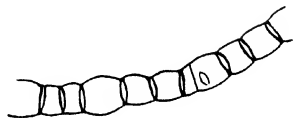
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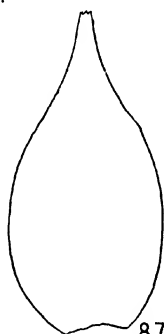
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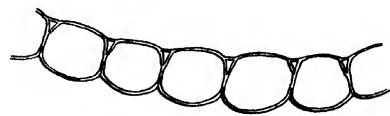
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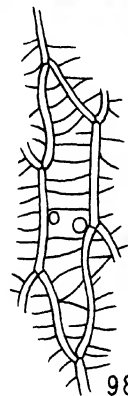
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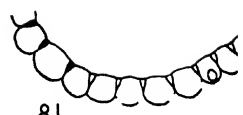
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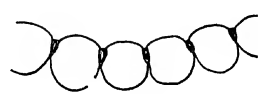
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# THE CLASSIFICATION OF CORRELATIONS IN SPACE

By E. T. BROWNE

1. *Introduction.* A correlation in space is a projective correspondence between the points and the planes of space such that all the planes through a point correspond to all the points on a plane. Analytically, a correlation in space is defined by equations of the type

$$(1) \quad \rho u_i = \Sigma a_{ij} x_j, \quad (i = 1, \dots, 4; \Delta = |a_{ij}| \neq 0),$$

where  $(x_1, x_2, x_3, x_4)$  are the homogeneous coördinates of a point  $x$ ,  $(u_1, u_2, u_3, u_4)$  are the coördinates of the corresponding plane  $u$ , and the frame of reference is thought of as being so chosen that the condition for united position of  $u$  and  $x$  is

$$\Sigma u_i x_i = 0.$$

On solving the equations (1) for the  $x$ 's in terms of the  $u$ 's, we have

$$(1') \quad \sigma x_i = \Sigma A_{ji} u_j \quad (i = 1, \dots, 4),$$

where  $A_{ij}$  is the cofactor of  $a_{ij}$  in the determinant  $\Delta$ . The equations (1') serve also to determine the correlation.

Suppose now that the plane  $u$  turns about a fixed but arbitrary point  $(y_1, y_2, y_3, y_4)$  so that we have

$$\rho \Sigma u_i y_i = \Sigma a_{ij} y_i x_j = 0.$$

From this it appears that the corresponding point  $x$  lies on the plane  $v$ , where

$$\tau v_j = \Sigma a_{ij} y_i,$$

or

$$(2) \quad \tau v_i = \Sigma a_{ji} y_j.$$

This plane  $v$  will coincide with the plane which corresponds to  $y$  under (1) if, and only if, there exists a number  $\lambda \neq 0$  such that

$$\Sigma a_{ij} y_j = \lambda \Sigma a_{ji} y_j,$$

or

$$(3) \quad \Sigma (a_{ij} - \lambda a_{ji}) y_j = 0 \quad (i = 1, \dots, 4).$$

In order that such a point  $y$  may arise it is necessary and sufficient that  $\lambda$  be so chosen that the determinant  $|A - \lambda A'|$  vanish; i.e., that  $\lambda$  be a root of the equation

$$(4) \quad D(\lambda) \equiv |A - \lambda A'| = \begin{vmatrix} a_{11} - \lambda a_{11} & \cdots & a_{11} - \lambda a_{41} \\ \cdots & \cdots & \cdots \\ a_{41} - \lambda a_{14} & \cdots & a_{44} - \lambda a_{44} \end{vmatrix} = 0.$$

Similarly, as the point  $x$  moves about in a plane  $v$ , the plane  $u$  corresponding to  $x$  will turn about the point  $y$  which corresponds to  $v$  under (1') if, and only if, there exists a number  $\lambda \neq 0$  such that

$$(5) \quad \Sigma(A_{ij} - \lambda A_{ji})v_j = 0. \quad (i = 1, \dots, 4).$$

That is,  $\lambda$  must be a root of the equation

$$(6) \quad \bar{D}(\lambda) = |(A^{-1})' - \lambda A^{-1}| = 0,$$

where  $(A^{-1})'$  is the transpose of the inverse of  $A$ .

The equations (4) and (6) are equivalent. For from the matricial relation

$$(7) \quad A - \lambda A' = A'[(A^{-1})' - \lambda A^{-1}]A,$$

we have on taking determinants

$$D(\lambda) = |A|^2 \cdot \bar{D}(\lambda).$$

Moreover, it is obvious from (7) that the matrices  $A - \lambda A'$  and  $(A^{-1})' - \lambda A^{-1}$  are of the same rank, so that there are just as many linearly independent planes  $v$  satisfying (5) as there are points  $y$  satisfying (3).

Suppose now that  $y$  is a point satisfying (3) and that  $v$  is the plane corresponding to  $y$  under (1); i.e.,

$$(3) \quad \Sigma a_{ij}y_j = \lambda \Sigma a_{ji}y_j,$$

$$(8) \quad \Sigma a_{ij}y_j = \rho v_i$$

On substituting  $\rho v_i$  for the left member of (3), multiplying through by  $A_{\tau i}$  and summing as to  $i$ , we get

$$\rho \Sigma A_{\tau i}v_i = \lambda \Sigma \Sigma A_{\tau i}a_{ji}y_j = \lambda |A| y_{\tau}.$$

But from (8) we have on multiplying through by  $A_{i\tau}$  and summing as to  $i$ ,

$$|A| y_{\tau} = \rho \Sigma A_{i\tau}v_i,$$

whence

$$\Sigma(A_{ri} - \lambda A_{ir})v_i = 0.$$

That is, if  $y$  is a point satisfying (3), its corresponding plane  $v$  satisfies (5) with the same value of  $\lambda$ . Such a pair  $(y, v)$  we call a double pair of the correlation arising from the root  $\lambda$ .<sup>1</sup>

2. *Projectively Equivalent Correlations.* Suppose now that the points and planes of space be referred to a different tetrahedron of reference. The coördinates  $x$  and the coördinates  $x'$  of the same point referred to the two different frames are connected by relations of the type

$$(9) \quad \tau x_i = \Sigma p_{ij} x'_j \quad |P| = |p_{ij}| \neq 0.$$

Moreover, the relations between the coördinates  $u$  and the coördinates  $u'$  of a plane referred to the two frames are

$$(9') \quad t' u_i = \Sigma P_{ij} u'_j,$$

where  $P_{ij}$  is the cofactor of  $p_{ij}$  in the determinant  $|P|$ . On eliminating the  $u$ 's and  $x$ 's from (1), (9) and (9'), we obtain

$$(10) \quad \rho' u'_i = \Sigma q_{ij} x'_j,$$

where the matrix  $Q$  is equal to  $P'AP$ .

The equations (10) may be thought of either as defining the correlation (1), the points and planes of space now being referred to a new frame of reference, or as defining a correlation projectively equivalent to (1), the frame of reference being the same.

Conversely, a correlation (1) of matrix  $A$  and a correlation (10) of matrix  $Q$  will be projectively equivalent if, and only if, there exists a non-singular matrix  $P$  such that  $Q = P'AP$ ; i.e., if and only if the matrices  $A$  and  $Q$  are congruent.<sup>2</sup>

3. *The Work of Kronecker and Segre.* Kronecker<sup>3</sup> has shown that two non-singular square matrices  $A$  and  $Q$  of the same order will be

<sup>1</sup> It is clear that the equations (2) also determine a correlation which has as its matrix the transpose matrix  $A'$  of  $A$ , and which will therefore be identical with (1) if, and only if,  $A$  is symmetric. We call (2) the correlation induced by (1). By reference to (3) and (5) it is easy to see that a double pair  $(y, v)$  of (1) will be a double pair of (2) also. Moreover, by the symmetry of the formulas and equations with respect to  $A$  and  $A'$ , it will follow that the two quadrics, shown subsequently to be associated with (1), will coincide with those associated with (2), and that the properties of the two correlations are identical. We shall therefore confine our attention to (1) only.

<sup>2</sup> Muth, *Theorie und Anwendung der Elementartheiler*, Leipzig, 1899, p. 142.

<sup>3</sup> Muth, *loc. cit.*, p. 143; cf. also Kronecker, *Über die congruenten Transformationen der bilinearen Formen*, Werke, Vol. I, pp. 424-483.



congruent if, and only if, there exist two non-singular matrices  $R$  and  $S$  such that

$$Q - \lambda Q' = R(A - \lambda A')S,$$

and hence, if and only if the two  $\lambda$ -matrices  $Q - \lambda Q'$ ,  $A - \lambda A'$  have the same elementary divisors. The problem of determining whether or not two correlations are projectively equivalent is reduced therefore to a problem in the theory of elementary divisors. By means of this theory it is shown that there are 15 distinct types of non-singular correlations in space, while among correlations of the same type there may be some which are projectively non-equivalent. The normal forms of these types are listed by Muth.<sup>4</sup>

The algebraic work of Kronecker has been interpreted geometrically by Segre,<sup>5</sup> who gives the geometric properties, both from the point of view of line geometry and from the point of view of the ordinary geometry of point and plane.

4. *Purpose of this paper.* It is the purpose of this paper to give a projective classification of non-singular correlations in space without making any use of the theory of elementary divisors. Such classifications for correlations in the plane are well known, such for example, as that given by Woods,<sup>6</sup> and the one given quite recently by the author and C. A. Denson.<sup>7</sup> The method employed here is an extension to three dimensions of that employed in the latter paper. The classification is made on the basis of certain invariants, the roots of the equation  $D(\lambda) = |A - \lambda A'| = 0$ , and the rank of the associated matrix  $A - \lambda A'$ , and on the mutual relationship between two associated quadrics. We do not attempt to develop criteria for distinguishing between two non-equivalent correlations of the same type, although it will follow from Kronecker's theory that the distinction can be made very readily through the roots of  $D(\lambda) = 0$ . Our purpose is merely to establish certain very simple tests whereby it can be determined to which of the 15 types a given correlation belongs, and in addition

<sup>4</sup> Muth, *loc. cit.*, p. 150.

<sup>5</sup> Segre, *Ricerche sulle omografie e sulle correlazioni in generale*, Mem. della Acc. delle Scienze di Torino, Ser. 2, Vol. 37 (1886), pp. 395-435.

<sup>6</sup> Woods, *Higher Geometry*, Boston (1922), pp. 88-94.

<sup>7</sup> *The Classification of Correlations in the Plane*, American Mathematical Monthly, Vol. 44 (1937), pp. 566-573

to derive in somewhat greater detail the geometric properties of each type which for the most part are merely listed by Segre.

5. *The Quadrics  $S$  and  $\Sigma$ ; Points and Planes of Double Pairs.* Much of the preliminary discussion necessary for a classification of correlations in space can be taken over almost bodily from the corresponding discussion for the plane. Indeed, if in the aforementioned paper,<sup>8</sup> the word *plane* be substituted for *line*, *quadric* be substituted for *conic*, and the summation range be extended from 1 to 4 instead of from 1 to 3, it will be easy to see that the proofs remain valid in the extended domain. We shall therefore merely state the following theorems:

**THEOREM I.** *A point  $x$  and the plane  $u$  corresponding to it under (1) will be in united position if, and only if,  $x$  is a point of a quadric  $S$  of matrix  $\frac{1}{2}(A + A')$ , and  $u$  is a plane of a quadric  $\Sigma$  of matrix  $\frac{1}{2}[A^{-1} + (A^{-1})']$ . The quadrics  $S$  and  $\Sigma$  are of the same rank.*

**THEOREM II.** *A point  $y$  and a plane  $v$  of a double pair  $(y, v)$  arising from a root  $\lambda \neq 1$  of  $D(\lambda) = 0$  are always in united position;  $y$  is therefore a point of  $S$  and  $v$  is a plane of  $\Sigma$ .*

**THEOREM III.** *If  $-1$  is a root of the equation  $D(\lambda) = 0$ , the quadric  $S(\Sigma)$  is singular and the point  $y$  (plane  $v$ ) of the double pair  $(y, v)$  arising from the root  $-1$  is a singular point (plane) of the surface.*

**THEOREM IV.** *If  $y$  and  $v$  are point and plane of a double pair  $(y, v)$  arising from a root  $\lambda \neq -1$  of  $D(\lambda) = 0$ , then  $y$  and  $v$  are pole and polar as to the quadrics  $S$  and  $\Sigma$ . In particular, if  $y$  is a point of  $S$  and therefore  $v$  a plane of  $\Sigma$ , then  $v$  is a common tangent plane to  $S$  and  $\Sigma$  at the point  $y$ .*

**THEOREM V.** *If  $y$  and  $v$  are point and plane of a double pair  $(y, v)$  arising from a root  $\lambda \neq \pm 1$  of  $D(\lambda) = 0$ , then  $v$  is a common tangent plane to  $S$  and  $\Sigma$  at  $y$ .*

Just as in the case of correlations in the plane, so also here it is evident at once by reference to equation (17) below that the equation  $D(\lambda) = 0$  is a reciprocal equation. However, we append here a proof that is valid for a non-singular matrix  $A$  of any finite order  $n$ .

**THEOREM VI.** *If  $A$  is a non-singular matrix of order  $n$ , the equation  $D(\lambda) = |A - \lambda A'| = 0$  is a reciprocal equation.*

<sup>8</sup> American Mathematical Monthly, Vol. 44, loc. cit., pp. 566-573.

Since by hypothesis  $A$  is non-singular, the equation  $D(\lambda) = 0$  cannot have the root  $\lambda = 0$ . Transposing the determinant about its main diagonal, we have

$$D(\lambda) = |A' - \lambda A| = (-\lambda)^n - \frac{1}{\lambda} A' + A = (-\lambda)^n D\left(\frac{1}{\lambda}\right).$$

The theorem is therefore proved.

We now establish two theorems that were not proved in the previous paper.

**THEOREM VII.** *If  $(y, v)$  and  $(y', v')$  are two double pairs arising from the roots  $\lambda$  and  $\lambda'$ , respectively, of  $D(\lambda) = 0$ , and if  $\lambda' \neq \frac{1}{\lambda}$ , then  $y$  lies on  $v'$  and  $y'$  lies on  $v$ .*

From (3) we have

$$\sum a_{ij} y_j = \lambda \sum a_{ij} y_j,$$

$$\sum a_{ij} y'_j = \lambda' \sum a_{ij} y'_j.$$

Multiply the first of these equations through by  $y'_i$  and sum as to  $i$ ; similarly, multiply the second through by  $y_i$  and sum as to  $i$ . We then have

$$\sum a_{ij} y'_i y_j = \lambda \sum a_{ij} y'_i y_j = \lambda \sum a_{ij} y_i y'_j;$$

$$\sum a_{ij} y_i y'_j = \lambda' \sum a_{ij} y_i y'_j = \lambda' \sum a_{ij} y'_i y_j.$$

Combining these last two equations, we have

$$\sum a_{ij} y'_i y_j = \lambda \lambda' \sum a_{ij} y'_i y_j,$$

whence, since  $\lambda \lambda' \neq 1$ ,

$$\sum a_{ij} y'_i y_j = 0.$$

By reference to (1) it is seen that this is precisely the condition that  $y'$  lie on  $v$ . Similarly,  $y$  lies on  $v'$ .

**THEOREM VIII.** *If  $\rho$  is a root  $\neq \pm 1$  of  $D(\lambda) = 0$  and if the matrix  $A - \rho A'$  is of rank 3, the plane  $v$  of the double pair  $(y, v)$  arising from the root  $\rho$  will pass through the point  $y'$  of the double pair  $(y', v')$  arising from the root  $\frac{1}{\rho}$  if, and only if,  $\rho$  is a multiple root of  $D(\lambda) = 0$ .*

The matrices  $A - \rho A'$  and  $A - \frac{1}{\rho} A'$  are obviously of the same rank

so that there is a single point  $y'$  and a single plane  $v'$  arising from the root  $\frac{1}{\rho}$ . Let us now choose the point  $y$  as the vertex  $(1,0,0,0)$  of our tetrahedron of reference. Since by hypothesis  $\rho \neq \pm 1$ , by Theorem II  $v$  passes through  $y$ . We may then choose  $v$  as the plane  $x_4 = 0$ . By using equations (1) and (3) it is then easy to verify that the matrix  $A$  of the correlation will be of the form:

$$A = \begin{pmatrix} 0 & 0 & 0 & a_{14} \\ 0 & a_{22} & a_{23} & a_{24} \\ 0 & a_{32} & a_{33} & a_{34} \\ \rho a_{14} & a_{42} & a_{43} & a_{44} \end{pmatrix} \quad (a_{14} \neq 0).$$

If for this matrix we form the determinant  $|A - \lambda A'|$ , we find that

$$D(\lambda) = -a_{14}^2(\rho - \lambda)(1 - \rho\lambda) F(\lambda),$$

where

$$F(\lambda) = \begin{vmatrix} a_{22}(1 - \lambda) & a_{23} - \lambda a_{32} \\ a_{32} - \lambda a_{23} & a_{33}(1 - \lambda) \end{vmatrix}.$$

The coördinates  $(y'_1, y'_2, y'_3, y'_4)$  of the point  $y'$  arising from the root  $\frac{1}{\rho}$  are proportional to the cofactors of the elements in the first row of  $A - \frac{1}{\rho} A'$ . We may therefore take as  $y'_4$ :

$$y'_4 = -a_{14} \left( \rho - \frac{1}{\rho} \right) F\left(\frac{1}{\rho}\right).$$

Since  $\rho \neq \pm 1$ , this point will lie on the plane  $x_4 = 0$  if, and only if,  $F\left(\frac{1}{\rho}\right) = 0$ ; i.e.,  $\frac{1}{\rho}$ , and hence  $\rho$ , is a multiple root of  $D(\lambda) = 0$ .

6. *Canonical Form for the Matrix of a Non-singular Correlation.* Since the matrix  $B = \frac{1}{2}(A + A')$  of the quadric surface  $S$  is symmetric, there exists a non-singular matrix  $P$  such that  $P'BP = N$ , where  $N$  consists of zeros except in the diagonal. The elements in the diagonal of  $N$  are the coefficients  $a, b, c, d$  in the canonical equation of  $S$ :

$$(11) \quad ax_1^2 + bx_2^2 + cx_3^2 + dx_4^2 = 0.$$

Geometrically, this means that we have chosen as tetrahedron of reference a self-polar tetrahedron with respect to  $S$ .<sup>9</sup> Since  $C = \frac{1}{2}(A - A')$  is skew symmetric, so also is  $P'CP$ . Hence  $P'AP = P'(B + C)P$  is of the form:

$$(12) \quad P'AP = \begin{pmatrix} a & h & -g & l \\ -h & b & f & m \\ g & -f & c & n \\ -l & -m & -n & d \end{pmatrix},$$

where

$$(13) \quad \Delta = abcd + (abn^2 + acm^2 + bcl^2 + adf^2 + bdg^2 + cdh^2) + (fl + gm + hn)^2 \neq 0.$$

Hence, (12) is a canonical form to which the matrix of any non-singular space correlation can be reduced. With  $A$  in this form, the matrix  $A - \lambda A'$  assumes the simple form:

$$(14) \quad A - \lambda A' = \begin{pmatrix} a(1 - \lambda) & h(1 + \lambda) & -g(1 + \lambda) & l(1 + \lambda) \\ -h(1 + \lambda) & b(1 - \lambda) & f(1 + \lambda) & m(1 + \lambda) \\ g(1 + \lambda) & -f(1 + \lambda) & c(1 - \lambda) & n(1 + \lambda) \\ -l(1 + \lambda) & -m(1 + \lambda) & -n(1 + \lambda) & d(1 - \lambda) \end{pmatrix}.$$

If now for brevity we denote by  $\varphi$  and  $K$  the expressions

$$(15) \quad \varphi = abn^2 + acm^2 + bcl^2 + adf^2 + bdg^2 + cdh^2,$$

$$(16) \quad K = fl + gm + hn,$$

we have

$$(13') \quad \Delta = abcd + \varphi + K^2$$

and

$$(17) \quad D(\lambda) = abcd(1 - \lambda)^4 + \varphi(1 - \lambda)^2(1 + \lambda)^2 + K^2(1 + \lambda)^4.$$

<sup>9</sup> Bôcher, *Introduction to Higher Algebra*, New York, (1907), pp. 124-125.

It can now be verified at the expense of some computation that with  $A$  in the form (12), the matrix  $A^{-1} + (A^{-1})'$  of the quadric  $\Sigma$  in plane coördinates is

$$(18) \quad \Sigma: \begin{pmatrix} bcd + bn^2 + cm^2 + df^2 & dfg - clm & & & \\ dfg - clm & acd + an^2 + cl^2 + dg^2 & & & \\ dfh - bln & dgh - amn & & & \\ chm - bgn & afn - chl & & & \\ & dfh - bln & chm - bgn & & \\ & dgh - amn & afn - chl & & \\ & abd + am^2 + bl^2 + dh^2 & bgl - afm & & \\ & bgl - afm & abc + af^2 + bg^2 + ch^2 & & \end{pmatrix}$$

7. *Conditions that the Quadrics  $S$  and  $\Sigma$  Coincide.* Let us suppose that  $abcd \neq 0$  so that  $S$  and  $\Sigma$  are non-singular quadrics. The equation of  $S$  in plane coördinates is then

$$\hat{S}: \quad bcd u_1^2 + acd u_2^2 + abdu_3^2 + abc u_4^2 = 0.$$

It is clear then that  $S$  and  $\Sigma$  will coincide if, and only if,

$$(19) \quad \begin{aligned} dfg &= clm & dgh &= amn \\ dfh &= bln & afn &= chl \\ chm &= bgn & bgl &= afm, \end{aligned}$$

and in addition there exists a number  $\tau \neq 0$  such that

$$(20) \quad \begin{aligned} bcd(1 - \tau) + bn^2 + cm^2 + df^2 &= 0, \\ acd(1 - \tau) + an^2 + cl^2 + dg^2 &= 0, \\ abd(1 - \tau) + am^2 + bl^2 + dh^2 &= 0, \\ abc(1 - \tau) + af^2 + bg^2 + ch^2 &= 0. \end{aligned}$$

We may state these results in the form of a theorem.

**THEOREM IX.** *If  $abcd \neq 0$ , the quadrics  $S$  and  $\Sigma$  will coincide if, and only if, the conditions (19) hold, and in addition there exists a number  $\tau \neq 0$  such that (20) holds.*

8. *Enumeration of Cases.* From (17) it is clear that  $\lambda = 1$  is a root of  $D(\lambda) = 0$  if, and only if,  $K = 0$ , in which case 1 is at least a double root. Similarly,  $-1$  is a root if, and only if,  $abcd = 0$  in which case

this root is at least a double root. On reflection it will be clear that the following cases, and these only, can arise:

Case I.  $D(\lambda) = 0$  has the roots 1, 1, 1, 1. Then  $\varphi = 0$ ,  $K = 0$ ,  $abcd \neq 0$ .

Case II.  $D(\lambda) = 0$  has the roots 1, 1, -1, -1. Then  $K = 0$ ,  $\varphi \neq 0$ ,  $abcd = 0$ , but  $(a, b, c, d) \neq (0, 0, 0, 0)$ .

Case III.  $D(\lambda) = 0$  has the roots -1, -1, -1, -1. Then  $abcd = 0$ ,  $\varphi = 0$ ,  $K \neq 0$ .

Case IV.  $D(\lambda) = 0$  has the roots 1, 1,  $\lambda$ ,  $\frac{1}{\lambda}$ ; ( $\lambda \neq \pm 1$ ). Here  $abcd \neq 0$ ,  $\varphi \neq 0$ ,  $K = 0$ . If we write  $\frac{1 - \lambda}{1 + \lambda} = \mu$ , ( $0 \neq \mu \neq \pm 1$ ) then  $\mu$  is a root of the quadratic

$$(21) \quad abcd\mu^2 + \varphi = 0.$$

Note that replacing  $\mu$  by  $-\mu$  replaces  $\lambda$  by  $\frac{1}{\lambda}$ .

Case V.  $D(\lambda) = 0$  has the roots -1, -1,  $\lambda$ ,  $\frac{1}{\lambda}$ ; ( $\lambda \neq \pm 1$ ). Here  $\varphi \neq 0$ ,  $K \neq 0$ ,  $abcd = 0$ , but  $(a, b, c, d) \neq (0, 0, 0, 0)$ . Also  $\mu = \frac{1 - \lambda}{1 + \lambda}$  is a root of

$$(22) \quad \varphi\mu^2 + K^2 = 0.$$

Case VI.  $D(\lambda) = 0$  has the roots  $\lambda$ ,  $\frac{1}{\lambda}$ ,  $\lambda$ ,  $\frac{1}{\lambda}$ . Here  $abcd \neq 0$ ,  $\varphi \neq 0$ ,  $K \neq 0$ , and the equation

$$(23) \quad abcd\mu^4 + \varphi\mu^2 + K^2 = 0$$

considered as a quadratic in  $\mu^2$  has a double root; i.e.,

$$(24) \quad \varphi^2 - 4abcdK^2 = 0.$$

Case VII.  $D(\lambda) = 0$  has the roots  $\lambda_1$ ,  $\frac{1}{\lambda_1}$ ,  $\lambda_2$ ,  $\frac{1}{\lambda_2}$ . Here we have the same conditions as in Case VI, except that the quadratic (23) in  $\mu^2$  has distinct roots.

These seven cases subdivide further according to the rank of the associated matrix  $A - \lambda A'$  and to the mutual relationship of the quadrics  $S$  and  $\Sigma$ . In fact, as we shall see, there are 15 distinct types of correlations in space. In order to facilitate comparison of the cases

as arrived at here with the canonical forms as listed by Muth, we shall in each case refer to the number of the corresponding form given by Muth, *loc. cit.*, p. 150.

9. Case I.  $D(\lambda) = 0$  has the roots 1,1,1,1. Since  $abcd \neq 0$ , the quadrics  $S$  and  $\Sigma$  are non-singular. All points of double pairs are obtained by solving the equations (3) with  $\lambda = 1$ . The matrix  $A - A'$  of this system is skew-symmetric, its determinant being  $16K^2 = 0$ . Hence the rank of the matrix is 0 or 2.<sup>10</sup>

Case I-1. If the matrix  $A - A'$  is of rank 0, then  $f, g, h, l, m, n$  are all zero. The matrix  $A$  of the correlation is therefore symmetric. Moreover, the conditions (19) and (20) are obviously satisfied, the latter with  $\tau = 1$ , so that the quadrics  $S$  and  $\Sigma$  coincide. Every point  $y$  in space is a point of a double pair  $(y, v)$ , the plane  $v$  corresponding to  $y$  being the polar plane of  $y$  as to  $S$ . This is the so-called *polarity*.<sup>11</sup> It is Muth's case 11.

Case I-2. Suppose next that the matrix  $A - A'$  is of rank 2. Then since  $f, g, h, l, m, n$  are not all zero, it is a matter of notation to suppose that  $h \neq 0$ . There is an entire line  $L$  of points  $y$  of double pairs  $(y, v)$ , the equations of which may be taken as

$$\begin{aligned} (25) \quad L: \quad & hx_2 - gx_3 + lx_4 = 0 \\ & -hx_1 + fx_3 + mx_4 = 0. \end{aligned}$$

In terms of the parameters  $\xi, \eta$  the coördinates of a typical point  $y$  on  $L$  may be written:

$$(26) \quad y: \quad (f\xi + m\eta, g\xi - l\eta, h\xi, h\eta).$$

By Theorem IV the plane  $v$  corresponding to  $y$  under the correlation is the polar plane of  $y$  as to  $S$ ; i.e.,

$$(27) \quad v: \quad (af\xi + am\eta, bg\xi - bl\eta, ch\xi, dh\eta).$$

As  $y$  runs along  $L$ ,  $v$  turns about the line  $M$

$$\begin{aligned} (28) \quad M: \quad & afx_1 + bgx_2 + chx_3 = 0 \\ & amx_1 - blx_2 + dhx_4 = 0, \end{aligned}$$

which is the conjugate line of  $L$  as to  $S$ .

<sup>10</sup> Bôcher, *loc. cit.*, Ex. 4, p. 59.

<sup>11</sup> Woods, *loc. cit.*, p. 247.



The lines  $L$  and  $M$  have at least one point in common, the coördinates of which may be taken as any one of the following sets which does not consist entirely of zeros:

$$T: \begin{array}{cccc} (bn^2 + cm^2 + df^2, & dfg - clm, & dfh - bln, & chm - bgn) \\ (dfg - clm, & an^2 + cl^2 + dg^2, & dgh - amn, & afn - chl) \\ (dfh - bln, & dgh - amn, & am^2 + bl^2 + dh^2, & bgl - afm) \\ (chm - bgn, & afn - chl, & bgl - afm, & af^2 + bg^2 + ch^2) \end{array}$$

If all of the above sets vanish,  $L$  coincides with  $M$ . Moreover, the conditions (19) and (20) are evidently satisfied, the latter with  $\tau = 1$ , so that by Theorem IX the quadrics  $S$  and  $\Sigma$  coincide. Conversely, if the quadrics coincide the lines  $L$  and  $M$  are identical.

Both of the foregoing situations actually arise and we have a separation of cases.

Case I-21. Here the quadrics  $S$  and  $\Sigma$  coincide. There is a line  $L$  (25) of points of double pairs which is a generator of  $S$  and as the point  $y$  moves along  $L$ , its corresponding plane  $v$  turns about  $L$ . This is Muth's Case 14.

Case I-22. Here the quadrics  $S$  and  $\Sigma$  do not coincide.  $L$  and  $M$  intersect in a unique point  $T$  which lies on  $S$ , and the tangent plane  $\pi$  to  $S$  at  $T$  is the plane of  $L$  and  $M$ . Hence, by Theorem IV,  $S$  and  $\Sigma$  are tangent to each other at  $T$ . But further from (18) and from the plane equation of  $S$  it can be verified that

$$\Sigma - \hat{S} = k(\Sigma\alpha_i u_i)^2,$$

where the  $\alpha$ 's are the coördinates of  $T$ .

If in §6, instead of so choosing the tetrahedron of reference that the equation of  $S$  is in canonical form, we should choose the tetrahedron so that the equation of  $\Sigma$  is in canonical form, the rôles of  $S$  and  $\Sigma$  would be interchanged. We can conclude then that if  $\hat{\Sigma} = 0$  is the point equation of  $\Sigma$ , then

$$\hat{\Sigma} - S = k'(\Sigma\beta_i x_i)^2,$$

where the  $\beta$ 's are the coördinates of the tangent plane  $\pi$  to  $S$  at  $T$ . Hence, the only points common to  $S$  and  $\Sigma$  are those in which  $\pi$  intersects  $S$ ; i.e., the two generators through  $T$ . It can be shown that the two quadrics are tangent along these two generators and that the lines  $L$  and  $M$  separate these two generators harmonically. This is Muth's Case 13.

It will be noted in the work that follows that in this one case only, *viz.*, in distinguishing between Cases I-21 and I-22, do we find it necessary to invoke the relationship between the quadrics  $S$  and  $\Sigma$ . In all other cases the types of correlations are distinguished from one another by the roots of the equation  $D(\lambda) = 0$  and the rank of the associated matrix  $A - \lambda A'$ .

10. Case II.  $D(\lambda) = 0$  has the roots 1, 1, -1, -1. Here  $K = 0$ ,  $abcd = 0$ ,  $\varphi \neq 0$ , and not more than two of  $a, b, c, d$  can be zero since  $\varphi \neq 0$ . There is a separation of cases according to the number of coefficients in (11) that vanish, i.e., according as the rank of  $S$  is 3 or 2.

Case II-1.  $a = 0$ ,  $bcd \neq 0$ ,  $\varphi = bcl^2 + bdg^2 + cdh^2 \neq 0$ .

Case II-2.  $a = b = 0$ ,  $cd \neq 0$ ,  $\varphi = cdh^2 \neq 0$ .

Case II-1. The quadrics  $S$  and  $\Sigma$  are of rank 3.  $S$  is a proper cone

$$(29) \quad bx_2^2 + cx_3^2 + dx_4^2 = 0,$$

with vertex  $V: (1, 0, 0, 0)$ . The matrix of  $\Sigma$  in plane coördinates is (18) with  $a = 0$ .  $\Sigma$  is a pencil of planes of the second order and the singular plane is  $v: (0, h, -g, l)$ , the plane corresponding to  $V$  under the correlation. Evidently  $v$  passes through  $V$ . But it is not a proper tangent plane to  $S$ . To show this, we note that  $h, g, l$  cannot all be zero since  $\varphi \neq 0$ . If then we assume that  $h \neq 0$ , the line joining the two distinct points  $(0, g, h, 0)$ ,  $(0, l, 0, -h)$  on  $v$  will be tangent to  $S$  if, and only if, the quadratic

$$(30) \quad b(\xi g + l)^2 + ch^2\xi^2 + dh^2 = 0$$

in  $\xi$  has equal roots. But the discriminant is

$$(31) \quad (bg^2 + ch^2)(bl^2 + dh^2) - b^2g^2l^2 = h^2\varphi \neq 0.$$

We seek now for points  $y$  of double pairs. Corresponding to the root 1 we find an entire line  $L$  of such points whose equations are given in (25). The planes corresponding to points on  $L$  all pass through the line  $M$  whose equations are given by (28) with  $a = 0$ ,

$$(28') \quad M: bgx_2 + chx_3 = 0, \quad -blx_2 + dhx_4 = 0.$$

$M$  passes through  $V$  but does not meet  $L$ . It is evident that  $L$  lies in the singular plane  $v$ , and since  $v$  is not tangent to  $S$ ,  $L$  is neither a tangent nor a ruling of  $S$ . There are, therefore, just two points,  $P$  and  $Q$ , which lie on their corresponding planes,  $p$  and  $q$ . These two

planes are tangent to  $S$  at  $P$  and  $Q$ , respectively, and it is easy to verify that they intersect in  $M$ .

Consider now the root  $-1$ . The matrix of the system (3) is then (14) with  $a = 0$  and  $\lambda = -1$ . This is evidently of rank 3, so that corresponding to the root  $-1$  there is a single point  $(1, 0, 0, 0)$  of a double pair. This point is precisely the vertex  $V$  of the cone  $S$ . This is Muth's case 10.

Case II-2. Here  $a = b = 0$ ,  $K = 0$ ,  $cdh^2 \neq 0$ . The quadrics  $S$  and  $\Sigma$  are of rank 2 so that  $S$  consists of two planes and  $\Sigma$  consists of two points. If in the matrix (12) we put  $a = b = 0$ ,  $c = \alpha^2$ ,  $d = -\beta^2$ , the equation of  $S$  becomes

$$S: \alpha^2 x_3^2 - \beta^2 x_4^2 = 0.$$

Hence,  $S$  degenerates into the two planes

$$(32) \quad \begin{aligned} \pi_1: \alpha x_3 - \beta x_4 &= 0, \\ \pi_2: \alpha x_3 + \beta x_4 &= 0, \end{aligned}$$

which intersect in the line  $M$ :  $x_3 = 0$ ,  $x_4 = 0$ . By referring to (18) it will be seen that the equation of  $\Sigma$  can be written

$$\Sigma: \alpha^2(mu_1 - lu_2 + hu_4)^2 - \beta^2(fu_1 + gu_2 + hu_3)^2 = 0,$$

so that the coördinates of the two points  $P_1$  and  $P_2$  of  $\Sigma$  are

$$(33) \quad \begin{aligned} P_1: (m\alpha + f\beta, -l\alpha + g\beta, h\beta, h\alpha) \\ P_2: (m\alpha - f\beta, -l\alpha - g\beta, -h\beta, h\alpha). \end{aligned}$$

Evidently  $P_1$  lies on  $\pi_1$  and  $P_2$  lies on  $\pi_2$ . Moreover,  $\pi_1$  and  $\pi_2$  correspond to  $P_1$  and  $P_2$ , respectively, under the correlation.

Let us now seek the points and planes of double pairs. Corresponding to the root  $\lambda = 1$ , we get as before a line  $L$  of points whose equations are given by (25). It is evident that  $L$  passes through  $P_1$  and  $P_2$ . As the point  $P$  whose coördinates are given by (26) moves along  $L$ , its corresponding plane

$$\alpha^2 \xi x_3 - \beta^2 \eta x_4 = 0$$

turns about the line  $M$  and intersects  $L$  in the point  $T$ :

$$(f\beta^2 \eta + m\alpha^2 \xi, g\beta^2 \eta - l\alpha^2 \xi, \beta^2 h\eta, \alpha^2 h\xi).$$

It is easy to verify that  $P$  and  $T$  separate  $P_1$  and  $P_2$  harmonically.

Since the matrix  $A + A'$  is the matrix (14) with  $a = b = 0$ ,  $\lambda = -1$ , its rank is 2, so that corresponding to the root  $-1$  there is a line of

points of double pairs, viz., the line  $M$ . As a point  $Q$  moves along  $M$ , the plane corresponding to  $Q$  passes through  $Q$  and turns about  $L$ . This is Muth's case 12.

11. Case III.  $D(\lambda) = 0$  has the roots  $-1, -1, -1, -1$ . Here  $abcd = 0, \varphi = 0, K \neq 0$ . There are four subcases.

Case III-1.  $a = 0, bcd \neq 0$ .

Case III-2.  $a = b = 0, cd \neq 0; \varphi = cdh^2 = 0, h = 0$ .

Case III-3.  $a = b = c = 0, d \neq 0$ .

Case III-4.  $a = b = c = d = 0$ .

Case III-1. The quadric  $S$  is a proper cone (29) with vertex  $V: (1, 0, 0, 0)$ .  $\Sigma$  is a pencil of planes of the second order, the singular plane being, as in Case II-1,  $v: (0, h, -g, l)$ .

Since  $\varphi = 0$ , the discriminant (31) of the quadratic (30) is zero, so that  $v$  is a proper tangent plane to  $S$ . If we denote by  $Q$  the point

$$Q: (0, cl^2 + dg^2, dgh, -chl),$$

it is easy to see that  $v$  is tangent to  $S$  along the line  $VQ$ , and, as a point  $P$  moves along  $VQ$ , the plane  $\pi$  corresponding to  $P$  turns about  $VQ$ .

The only point of a double pair is the vertex  $V$  of  $S$ , the plane corresponding to  $V$  being the singular plane  $v$  of  $\Sigma$ . This is Muth's case 8.

Case III-2.  $a = b = 0, cd \neq 0, K \neq 0$ . If, as in Case II-2, we put  $c = \alpha^2, d = -\beta^2$ , we have as the planes of  $S$  the two planes  $\pi_1$  and  $\pi_2$  in (32), while  $\Sigma$  consists of the two points  $P_1$  and  $P_2$  whose coördinates are obtained by putting  $h = 0$  in (33). The planes  $\pi_1$  and  $\pi_2$  correspond to  $P_1$  and  $P_2$ , respectively, under the correlation, and the line of intersection of the two planes is the line  $P_1P_2$ . This line is therefore a line of points of double pairs.

As a point  $Q$  moves about in the plane  $\pi_1$ , its corresponding plane passes through  $P_1$  and  $Q$ ; i.e., the plane turns about the line  $P_1Q$  as an instantaneous axis. This is Muth's case 7.

Case III-3.  $a = b = c = 0, d \neq 0, K \neq 0$ . The quadric  $S$  consists of the plane  $\pi: x_4 = 0$ , repeated. The quadric  $\Sigma$  consists of the point  $P: (f, g, h, 0)$ , repeated.  $P$  lies on  $\pi$  and corresponds to it under the correlation. Each point of  $\pi$  is a point of a double pair. The plane corresponding to a point  $Q$  of  $\pi$  passes through  $Q$  and  $P$ , i.e., as  $Q$  moves about in the plane  $\pi$ , the plane corresponding to  $Q$  turns about  $PQ$  as an instantaneous axis. This is Muth's case 9.

Case III-4.  $a = b = c = d = 0, K \neq 0$ . The quadrics  $S$  and  $\Sigma$  are of rank zero. We may then think of  $S$  as consisting of all points in space and of  $\Sigma$  as all planes in space. Every point  $P$  in space is a

point of a double pair  $(P, \pi)$ , where  $P$  lies on  $\pi$ . This is the *Null System* of Möbius,<sup>12</sup> and is Muth's case 15.

12. *Rank of the Matrix  $A - \lambda A'$  for  $\lambda \neq -1$ .* Before proceeding to a discussion of cases IV, V, VI and VII we shall find it desirable to establish a lemma. It is obvious that for  $\lambda \neq -1$ , the matrix  $A - \lambda A'$  in (14) can be written

$$(14') \quad A - \lambda A' = (1 + \lambda) \begin{pmatrix} a\mu & h & -g & l \\ -h & b\mu & f & m \\ g & -f & c\mu & n \\ -l & -m & -n & d\mu \end{pmatrix},$$

where  $\mu = \frac{1 - \lambda}{1 + \lambda}$ . If then  $\lambda$  is a root  $\neq -1$  of  $D(\lambda) = 0$ , we write  $D(\lambda) = (1 + \lambda)^4 F(\mu)$ , where

$$(17') \quad F(\mu) = abcd\mu^4 + \varphi\mu^2 + K^2.$$

We now prove the lemma:

*Lemma.* If  $\lambda \neq -1$  is a root of  $D(\lambda) = 0$ , the matrix  $A - \lambda A'$  on the right in (14') is of rank less than 3 only if  $\mu$  is a multiple root of (17').

For the third order principal minors of  $A - \lambda A'$  are, save for the factor  $(1 + \lambda)^3$ :

$$\mu(bcd\mu^2 + bn^2 + cm^2 + df^2),$$

$$\mu(acd\mu^2 + an^2 + cl^2 + dg^2),$$

$$\mu(abd\mu^2 + am^2 + bl^2 + dn^2),$$

$$\mu(abc\mu^2 + af^2 + bg^2 + ch^2).$$

If all these principal minors vanish, we have, on multiplying through by  $a, b, c$  and  $d$ , respectively, and adding,

$$4abcd\mu^3 + 2\varphi\mu = 0;$$

that is,  $F'(\mu) = 0$ , so that  $\mu$  is a multiple root of (17').

13. Case IV.  $D(\lambda) = 0$  has the roots  $1, 1, \lambda, \frac{1}{\lambda}$ ; ( $\lambda \neq \pm 1$ ). Here  $abcd \neq 0$ ,  $\varphi \neq 0$ ,  $K = 0$ . If  $\mu = \frac{1 - \lambda}{1 + \lambda}$ , then  $\mu$  is a root of

$$abcd\mu^2 + \varphi = 0.$$

<sup>12</sup> Woods, *loc. cit.*, p. 248.

The quadrics  $S$  and  $\Sigma$  are non-singular. Since  $\varphi \neq 0$ , we cannot have  $f, g, h, l, m, n$  all zero. Hence the matrix  $A - A'$  is of rank 2, so that corresponding to the root 1 there is a line  $L$  of points of double pairs, whose equations for  $h \neq 0$  are given by (25). As a point moves along  $L$ , its corresponding plane turns about a line  $M$  (28) which is conjugate to  $L$  with respect to  $S$ .  $L$  does not intersect  $M$ , neither is it tangent to  $S$ , since the discriminant (31) of the quadratic (30) is  $h^2\varphi \neq 0$ . Hence,  $L$  cuts  $S$  in two distinct points,  $T_1$  and  $T_2$ . The planes corresponding to  $T_1$  and  $T_2$  are by Theorem IV common tangent planes to  $S$  and  $\Sigma$  at  $T_1$  and  $T_2$ , respectively, and these planes intersect in  $M$ .

Consider now the roots  $\lambda$  and  $\frac{1}{\lambda}$ . By the lemma of the preceding section each of the matrices  $A - \lambda A'$  and  $A - \frac{1}{\lambda} A'$  is of rank 3, so that corresponding to each of the roots there is a single point of a double pair. By theorems II and IV, these points  $R_1$  and  $R_2$  lie on  $S$  and  $\Sigma$ , and the planes corresponding to them are common tangent planes to the two quadrics at  $R_1$  and  $R_2$ , respectively. By Theorem VII these two planes intersect in  $L$ . Also, by the same theorem, the tangent planes to  $S$  at  $T_1$  and  $T_2$  pass through both  $R_1$  and  $R_2$ , so that the latter two points are the points of intersection of  $M$  with  $S$  (and  $\Sigma$ ). The two quadrics therefore intersect along the four generators which form the sides of the skew quadrilateral  $R_1T_1R_2T_2$ , and are tangent at each of the vertices of the quadrilateral. This is Muth's case 6.

14. Case V.  $D(\lambda) = 0$  has the roots  $-1, -1, \lambda, \frac{1}{\lambda}$ ; ( $\lambda \neq \pm 1$ ). Here  $\varphi \neq 0, K \neq 0, abcd = 0$ , but not more than two of  $a, b, c, d$  can be zero since  $\varphi \neq 0$ . If as above we write  $\mu = \frac{1 - \lambda}{1 + \lambda}$ , then  $\mu$  is a root of the quadratic equation

$$\varphi\mu^2 + K^2 = 0.$$

Two subcases arise: 1.  $a = 0, bcd \neq 0$ ;

2.  $a = b = 0, cd \neq 0$ .

Case V-1. Here  $S$  and  $\Sigma$  are of rank 3. Hence,  $S$  is a proper cone with vertex  $V: (1, 0, 0, 0)$  as in case II-1. Similarly,  $\Sigma$  is a pencil of planes of the second order whose singular plane  $v: (0, h, -g, l)$  corre-

sponds to  $V$  under the correlation. The plane  $v$  passes through the vertex  $V$  of  $S$  but is not a proper tangent plane to  $S$ .

Corresponding to the root  $-1$  there is a single point  $V$  of a double pair  $(V, v)$ . Consider then the roots  $\lambda, \frac{1}{\lambda}$ . By the lemma of section 12,

the matrices  $A - \lambda A'$ ,  $A - \frac{1}{\lambda} A'$  are of rank 3, so that corresponding to each root there is a single point of a double pair. Each of these points  $R_1$  and  $R_2$  lies on one of the generators in which the plane  $v$  intersects  $S$ , and the tangent planes to  $S$  at  $R_1$  and  $R_2$  correspond to the latter under the correlation. This is Muth's case 4.

Case V-2.  $a = b = 0$ ,  $\varphi = cdh^2 \neq 0$ ,  $K \neq 0$ . The situation here is quite similar to that in case II-2.  $S$  degenerates into two planes  $\pi_1$  and  $\pi_2$ , while  $\Sigma$  degenerates into two points  $P_1$  and  $P_2$ .  $P_1$  lies on  $\pi_1$  and  $P_2$  lies on  $\pi_2$ . However, instead of a line  $L$  of points of double pairs arising from the double root  $\lambda = 1$ , here, arising from each of the roots  $\lambda, \frac{1}{\lambda}$ , there is a single point of a double pair. These points are precisely the points  $P_1$  and  $P_2$  of  $\Sigma$ . This is Muth's case 5.

15. Case VI.  $D(\lambda) = 0$  has the roots  $\rho, \frac{1}{\rho}, \rho, \frac{1}{\rho}$ , ( $\rho \neq \pm 1$ ). Hence  $abcd \neq 0$ ,  $\varphi \neq 0$ ,  $K \neq 0$ , and the quadratic

$$(23) \quad abcd\mu^4 + \varphi\mu^2 + K^2 = 0$$

in  $\mu^2$  has a double root.

The quadrics  $S$  and  $\Sigma$  are non-singular. In seeking for the points and planes of double pairs, it is evident that the matrix  $A - \lambda A'$  on the right in (14') can be of rank 1 only if

$$fl + gm = 0, \quad gm + hn = 0, \quad fl + hn = 0.$$

But on adding it would then follow that  $2K = 0$ , contrary to hypothesis. There is, however, a separation of cases according as the rank of this matrix is 2 or 3.

Case VI-1. The matrices  $A - \rho A'$ ,  $A - \frac{1}{\rho} A'$  of rank 2.

It can be shown without any difficulty that the matrix  $A - \rho A'$  will be of rank 2 if, and only if, the conditions (19) and (20) hold, the latter with  $1 - \tau$  replaced by  $\mu^2$ , and in addition we have

$$\begin{aligned} cdh\mu^2 + nK &= 0, & bdg\mu^2 + mK &= 0, & bcl\mu^2 + fK &= 0, \\ adf\mu^2 + lK &= 0, & acm\mu^2 + gK &= 0, & abn\mu^2 + hK &= 0. \end{aligned}$$

Under these conditions the quadrics  $S$  and  $\Sigma$  coincide. Corresponding to each of the roots  $\rho, \frac{1}{\rho}$ , there is a line of points of double pairs. These lines are by Theorem II rulings of  $S$ , and moreover they belong to the same regulus. For if they had a point in common we should have a point of a double pair arising from two distinct roots of  $D(\lambda) = 0$ . This is Muth's case 2.

Case VI-2. The matrices  $A - \rho A'$ ,  $A - \frac{1}{\rho} A'$  of rank 3. In this case the quadrics  $S$  and  $\Sigma$  do not coincide. Corresponding to each of the roots  $\rho, \frac{1}{\rho}$ , there is a single point of a double pair. These two points,  $P_1$  and  $P_2$ , lie on both  $S$  and  $\Sigma$ , and their corresponding planes,  $\pi_1$  and  $\pi_2$ , are common tangent planes to  $S$  and  $\Sigma$  at  $P_1$  and  $P_2$ , respectively. By Theorem VIII  $\pi_1$  passes through  $P_2$  and  $\pi_2$  passes through  $P_1$ . The line  $P_1P_2$  is a common ruling of  $S$  and  $\Sigma$  and the quadrics are tangent at each point of the ruling. This is Muth's case 3.

16. Case VII.  $D(\lambda) = 0$  has the roots  $\rho, \frac{1}{\rho}, \sigma, \frac{1}{\sigma}$ ; ( $\rho \neq \sigma \neq \pm 1$ ). Here  $abcd \neq 0, \varphi \neq 0, K \neq 0$ , while the quadratic (23) in  $\mu^2$  does not have a multiple root. The quadrics  $S$  and  $\Sigma$  are non-singular.

By the lemma of section 12 each of the matrices  $A - \rho A', \dots, A - \frac{1}{\sigma} A'$  is of rank 3, so that corresponding to each root of  $D(\lambda) = 0$  there is a single point of a double pair. Let  $(P_1, \pi_1), (P_2, \pi_2), (P_3, \pi_3), (P_4, \pi_4)$  be the double pairs arising from the roots  $\rho, \frac{1}{\rho}, \sigma, \frac{1}{\sigma}$ , respectively. Then by Theorem VII,  $\pi_1$  passes through  $P_3$  and  $P_4$ , but by Theorem VIII does not pass through  $P_2$ . Moreover, by Theorem V,  $P_1$  lies on both  $S$  and  $\Sigma$  and  $\pi_1$  is the common tangent plane to the two quadrics at  $P_1$ . A similar situation exists among the remaining points and planes of the double pairs. The four points  $P_1, P_2, P_3, P_4$  are therefore vertices of a skew quadrilateral whose sides are two generators from each regulus on  $S$ . Moreover, the two quadrics intersect along the above four rulings and are tangent to each other at each of the four points  $P$ . This is Muth's case 1.

17. *Summary.* Since under a transformation of the type (12) the determinant  $D(\lambda) = |A - \lambda A'|$  is an invariant of index 2, evidently



the roots of  $D(\lambda)$  are unaltered and the coefficients  $abcd$ ,  $\varphi$  and  $K^2$  are themselves invariants.<sup>12</sup> Let us as in section 6 write

$$B = \frac{1}{2}(A + A'), \quad C = \frac{1}{2}(A - A'),$$

Then since we can always, without loss of generality, so choose  $P$  in (12) that  $|P| = 1$ , it is clear that we can take

$$(34) \quad abcd = |B|, \quad K^2 = |C|,$$

whence from (13) it will follow that

$$(35) \quad \varphi = |A| - |B| - |C|.$$

Moreover, it is clear that the rank of  $B$  is precisely the number of the quantities  $a, b, c, d$  which are different from zero. The 15 cases which have been discussed in sections 8-16 can therefore be characterized completely as follows, it being assumed throughout that the correlation is non-singular, i.e., that  $|A| \neq 0$ .

Case I-1. The matrix  $A$  is symmetric; i.e.,  $C = 0$ .

Case I-21.  $|B| = |A|$ ;  $C$  of rank 2; and in addition the quadrics  $S$  and  $\Sigma$  coincide, i.e.,  $(A + A')^{-1} = k[A^{-1} + (A^{-1})']$ .

Case I-22. The same as in Case I-21, except that here the quadrics do not coincide.

Case II-1.  $B$  of rank 3,  $C$  of rank 2.

Case II-2.  $B$  of rank 2,  $C$  of rank 2.

Case III-1.  $B$  of rank 3,  $|C| = |A|$ .

Case III-2.  $B$  of rank 2,  $|C| = |A|$ .

Case III-3.  $B$  of rank 1,  $|C| = |A|$ .

Case III-4.  $B = 0$ , i.e.,  $A$  skew-symmetric.

Case IV.  $0 \neq |B| \neq |A|$ ;  $C$  of rank 2.

Case V-1.  $B$  of rank 3,  $|A| \neq |C| \neq 0$ .

Case V-2.  $B$  of rank 2,  $|A| \neq |C| \neq 0$ .

Case VI-1.  $B$  of rank 4,  $C$  of rank 4,  $\varphi = |A| - |B| - |C| \neq 0$   
 $\varphi^2 - 4|B||C| = 0$ ; i.e. the equation  $D(\lambda) = 0$  has the roots  $\rho, \frac{1}{\rho}, \rho,$

$\frac{1}{\rho}$  ( $\rho \neq \pm 1$ ), and the matrix  $A - \rho A'$  of rank 2.

Case VI-2. The same as in VI-1, except that the matrix  $A - \rho A'$  is of rank 3.

Case VII.  $B$  of rank 4,  $C$  of rank 4,  $\varphi \neq 0$ ,  $\varphi^2 - 4|B||C| \neq 0$   
 i.e., the equation  $D(\lambda) = 0$  has the roots  $\rho, \frac{1}{\rho}, \sigma, \frac{1}{\sigma}$ ; ( $\rho \neq \sigma \neq \pm 1$ ).

<sup>12</sup> Bôcher, *loc. cit.*, p. 166.

18. *Projective Equivalence of Correlations.* Up to this point in this paper, no use has been made of the results arrived at by Kronecker through the theory of elementary divisors. If, however, we refer to the canonical forms of non-singular correlations as listed by Muth, it will be seen that in each of the cases I-1, I-21, I-22, II-1, II-2, III-1, III-2, III-3, III-4 the canonical form contains no parameter, and hence that any two correlations belonging to one of these types are projectively equivalent. On the other hand, in each of the types IV, V-1, V-2, VI-1, VI-2 the canonical form contains a single parameter  $C_1$ , and in each case the equation  $D(\lambda) = 0$  has the roots  $C_1$  and  $\frac{1}{C_1}$ . Furthermore, in Case VII, Muth's canonical form contains two parameters  $C_1$  and  $C_2$ , while in this case the equation  $D(\lambda) = 0$  has precisely the roots  $C_1, \frac{1}{C_1}, C_2, \frac{1}{C_2}$ . This leads to the following theorem:

**THEOREM X.** *Two correlations belonging to one of the above 15 types are projectively equivalent if, and only if, their equations  $D(\lambda) = 0$  are equivalent.*

19. *Illustration.* Consider for example the correlation

$$\rho u = A(x),$$

in which

$$A = \begin{pmatrix} 5 & -6 & 5 & -4 \\ 10 & -1 & 5 & -1 \\ -1 & -1 & 0 & 0 \\ 4 & -1 & 2 & -1 \end{pmatrix}, \quad |A| = 9.$$

We find immediately that

$$B = \begin{pmatrix} 5 & 2 & 2 & 0 \\ 2 & -1 & 2 & -1 \\ 2 & 2 & 0 & 1 \\ 0 & -1 & 1 & -1 \end{pmatrix}, \quad C = \begin{pmatrix} 0 & -8 & 3 & -4 \\ 8 & 0 & 3 & 0 \\ -3 & -3 & 0 & -1 \\ 4 & 0 & 1 & 0 \end{pmatrix},$$

whence

$$|B| = abcd = 1, \quad |C| = K^2 = 16.$$

By (35) we find that  $\varphi = -8$ . Since all three of the quantities  $abcd$ ,  $K$ ,  $\varphi$  are different from zero, this correlation belongs either to type VI or to type VII. However, we see at once that

$$\varphi^2 - 4abcdK^2 = 0$$

so that the correlation belongs under type VI. The equation  $D(\lambda) = 0$  here is

$$(1 - \lambda)^4 - 8(1 - \lambda)^2(1 + \lambda)^2 + 16(1 + \lambda)^4 = 0,$$

the roots of which are  $-3$ ,  $-3$ ,  $-1/3$ ,  $-1/3$ . Moreover, the matrix  $A' + 3A'$  is found to be of rank 2. This definitely places the correlation under Case VI-1.

It is easy to verify that corresponding to each of the roots of  $D(\lambda) = 0$  the line of points of double pairs is a generator of  $S$  and that the quadrics  $S$  and  $\Sigma$  coincide.

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# INFLUENCE OF TEMPERATURE ON CYCLOMORPHOSIS OF DAPHNIA LONGISPINA<sup>1</sup>

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WITH 7 TEXT FIGURES

## I. HISTORICAL REVIEW

### *Cyclomorphosis*

Although Sars (1890), Zacharias (1893, 1894), and Lilljeborg (communication quoted by Zacharias, 1893) had noted the seasonal variation of certain Cladocera, it was Wesenberg-Lund (1900) who first made an extensive study of the cyclomorphosis of pelagic Cladocera, Protozoa, and Algae, and attempted to relate the seasonal changes to the physical conditions of the environment. Animals in summer may be so unlike their ancestors of the preceding winter, or their descendants of the following winter, that systematists have confidently placed them in different species or genera (*Daphnia* and *Hyalodaphnia*, or, among Protozoa, *Trachelius*, *Dileptus* and *Amphileptus*). The summer form is marked by elongation of the body, prolongations of the head to form "helmets" (fig. 1, *b*, *c*), spines, etc.—a strong development of the sort of structural features that have naturally suggested the designation "flotation processes." Wesenberg-Lund noted that the contrast of summer forms with winter forms was found only in pelagic organisms (and, as it then seemed, only in fresh-water plankton), not in those that live on the bottom or in the littoral. Among Cladocera, by the way, cyclomorphosis is featured by the females, not by the males, which occur only at certain times or under certain conditions.

### *Chief Theories as to the Significance and Causes of Cyclomorphosis in Cladocera*

It is not unnatural that explanations of the seasonal change of form should be sought in the contrasting physical conditions of the environment in winter and summer. Temperature, specific gravity, viscosity,

<sup>1</sup> Investigations aided by grant from the Rockefeller Fund for Research in Pure Science at the University of North Carolina.

gas content, nutrition would suggest themselves as possibly significant variables; the mineral content of the water could be eliminated as virtually unrelated to the season of the year, however much it might differ from lake to lake. Wesenberg-Lund concluded that it was the changing specific gravity of the water that governed this reversible metamorphosis from generation to generation—a series of changes aptly characterized by Woltereck later as *metagenetic* (as contrasted with ontogenetic or phylogenetic modifications).

W. Ostwald (1902) followed almost immediately with his more ambitious "Theory of the Plankton," in which he (1) analyzed the physical conditions of floating; (2) characterized the plankton as, by definition,

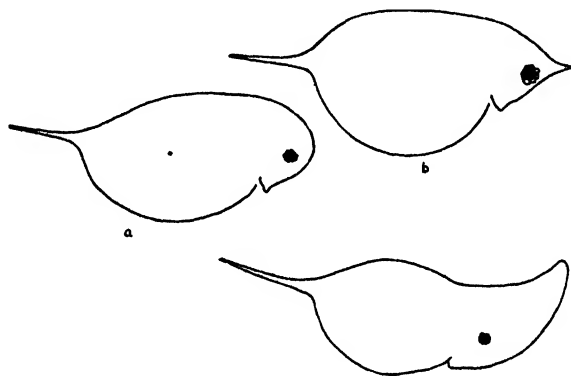


FIG. 1. a. *Daphnia longispina*, from University Lake, Chapel Hill, N. C., winter form (round head); b. same, late spring form (helmeted); c. *Daphnia* from Chautauqua Lake, N. Y., summer form.

made up of floating organisms and as possessing characteristic structural features (high water content with consequent translucency of body, oil-droplets, gas vacuoles, gelatinous hulls or bodily extensions in the forms of plates, keels, processes or long plumose setae which were sometimes remarkably developed); and (3) related such features to the continuing and changing conditions of flotation. Marine and fresh-water plankton came within his purview. Like Wesenberg-Lund, he considered the seasonal variations of fresh-water plankton organisms to be adaptations to the seasonal changes in the condition of flotation. Without going into the details of his argument, it is enough to say now that he dismissed specific gravity as the significant variable, since the changes were relatively small and would be parallel for organism and water,

and that he concluded that the changing viscosity of the water with seasonal change of temperature was the determining factor in cyclo-morphosis. Viscosity is practically doubled with a fall of 25° (25°–0°C.). Since we have to refer later to the seeming deficiency of records of precise experimental observation in all the literature that has followed, it should be mentioned here that Ostwald (1904) did conduct experiments with *Hyalodaphnia cristata* at different temperatures, although the conditions of his experiments seem to have been very unfavorable and the results, we should say now, quite inadequate to justify his conclusions.

Rearing *Hyalodaphnia cristata* at different temperatures very roughly controlled, he found that the young of short-helmeted individuals born at high temperatures had longer helmets than their parents and that the offspring of long-helmeted individuals born at low temperatures had shorter helmets than their parents. He was thus comparing young animals that passed through the embryonic stages under laboratory conditions with adults that had developed in the lake. Apparently he did not rear the young to ascertain if the helmets appropriate to the temperature were maintained throughout life at given temperatures, nor did he breed second generations. To an extent the results of his experiments were an indication of a relationship between temperature and form but they seem now to have afforded little support for his unqualified conclusion that seasonal variation in form was a result solely of temperature and that the expression "temporal (or seasonal) variation" should be replaced by "temperature variation" as the more precisely applicable term. It seems not to have been generally noted that Ostwald dealt with the form of the head of the newborn, while Woltereck later seems to have dealt chiefly with the form of the head of the developing young and adults. In nature, according to Wesenberg-Lund (1910), the changes occur chiefly from generation to generation and only to a lesser degree in the ontogeny of the free-swimming individuals. Causes of change may not be identical in the two cases.

Wesenberg-Lund accepted the emendation and the Wesenberg-Lund—Ostwald "Buoyance Theory" won general acceptance for a time; but Woltereck (1909, 1911, 1913, 1920, etc.), most notably, dissented. He found a significant weakness in the theory in that it failed to take proper account either (1) of the relation between the direction of extension of processes and the position of the animal in the water, or (2) of the self-propulsion of the animal. Ostwald had, indeed, considered vertical locomotion of plankton organisms, the energy required for

which was greater with diminished viscosity and consequently greater falling velocity, but he had discounted locomotion in a horizontal direction. In Woltereck's view, helmets, spines, mucros, etc., served like the keel and rudder of a ship as directing and guiding surfaces, whose functions were realized chiefly, if not exclusively, when the animal was in active movement, as it generally was. It was desirable for the animal to remain in a relatively thin layer of water where alone nutritive conditions were satisfactory during the summer period of stratification. The heightened cellular activity leading to the development of protuberances from the body was a more or less direct result of the better nutritive conditions and these protuberances, functioning as keels and rudders, enabled the animal to remain where the nutritive conditions were better.

Changing the viscosity of the medium by the addition of quince jelly had no effect.

Woltereck also introduced the "time factor" (Zeitfactor), measured by the generation number. He has held to the Weismannian idea of a definite reproductive cycle (ephippial egg—so many generations of parthenogenetic females—ephippial egg) now largely, if perhaps not completely, discredited by the work of Grosvenor and Smith (1913), Banta (1914, 1923, etc.), Berg (1932, 1934) and others, who relate the mode of reproduction to environmental conditions. The idea of the reproductive cycle implies that, after the ephippial or resting egg (a sexually fertilized egg), only so many generations (the number varying with the race) of parthenogenetic generations are possible before internal conditions require the production of ephippial eggs. The condition of sexuality, very weak in the exephippial generation, increases from parthenogenetic generation to parthenogenetic generation until it becomes commanding in respect to mode of reproduction.<sup>2</sup> The place of a particular animal in the cycle according to Woltereck was fixed by the number of generations from the ephippial egg—and its capacity to re-

<sup>2</sup> Another version of the reproductive cycle seems to be embodied in the "Depression" idea of Wagler (1923)—according to which there follows a diminution of vitality from generation to generation and from brood to brood—with an increasing tendency to production of males and ephippial females. This conception of a natural depression occurring automatically from internal causes may be contrasted with the view of Berg (1934) that "Depression" artificially produced by the accumulation of waste products or other causes leads to the incidence of sexual reproduction. The two views as to "Depression" really offer diametrically opposite explanations of the control of modes of reproduction, with evidence apparently favoring Berg's view.

act to the more abundant nutrition by change of form was determined in part by this number (fig. 2). The sixth generation with rich nour-

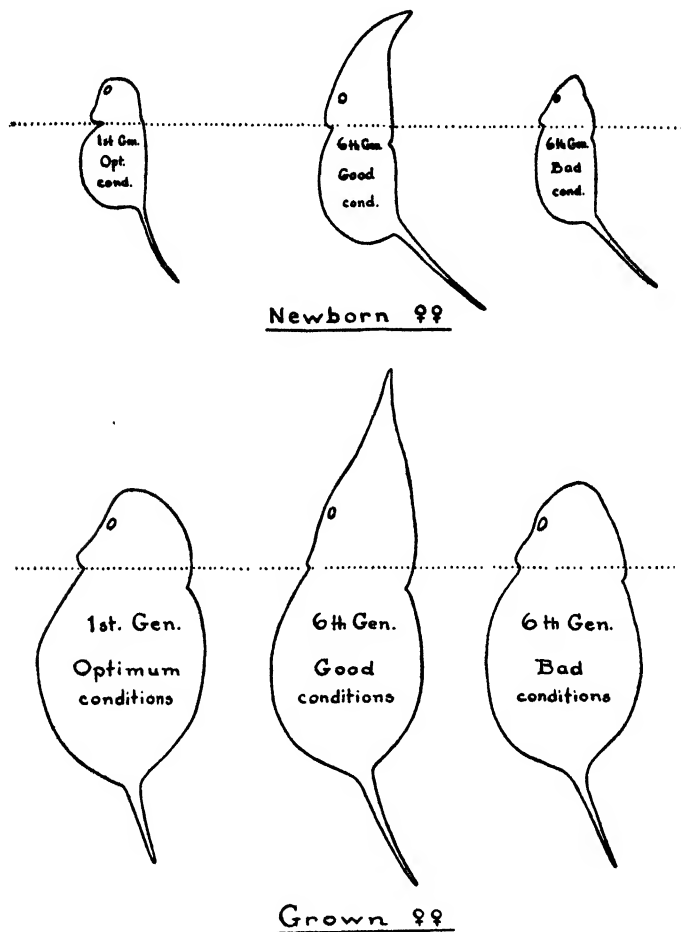


FIG. 2. *Daphnia cucullata*. Illustrating reported influence of conditions of nutrition and generation number on development of the helmet; adapted from Woltereck.

ishment would reproduce a high helmet (at low or high temperatures) but the first or second under like conditions would not.

It is quite impossible within narrow limits of space to review the prolonged discussion in literature where observation, experiment,



theory, argument, and speculation seem sometimes to be almost inextricably mixed. Nevertheless, in order measurably to clear the atmosphere and set the necessary background for our own experimental work, a further brief, if inadequate, review seems necessary.

Wesenberg-Lund's extensive and careful observations over a period of years in many waters, his synthesis of the observations made by himself and others, his recognition and statement of the problem were contributions of the highest value. He did not conduct experiments and has expressed himself as doubtful if experiments under laboratory conditions could be of much value with reference to his theory. Ostwald also contributed in a significant way by a more critical analysis of the physical factors involved in floating and by making the attempt, at least, to introduce the method of experiment. Woltereck's greatest contribution, undoubtedly, was in his classical study of the dynamics of locomotion of *Daphnia*, *Bosmina*, etc. (1913). He changed the aspect of the problem for active plankters from one in which statics too greatly predominated to one in which dynamics received proper consideration. It was not a question of how the animal is prevented from sinking in spite of its weak efforts to keep in the upper water, but rather one of how the animal keeps moving in a generally horizontal direction in spite of its own powerful strokes tending to force its head end upward and backward or vice versa, how it moves along under control at the preferred depth instead of vainly turning somersaults. Keels and rudders afford the answer. It is a fact, however, that the animal gets along in winter with greatly reduced keels and rudders. If the directive processes are necessary adaptations, the necessity must be far greater in summer than in winter. This seems to lead us back to temperature and to some associated quality of water that affects movement through the water—presumably density or viscosity.

Woltereck has evidently made extended use of the experimental method in breeding and rearing *Daphnias*, but, with respect to many questions, the results of his experiments cannot be effectively and critically availed of by others for lack of knowledge of the condition and precise results of his experiments. We should like to know if the animals were reared in isolation or in mass cultures, the precise temperatures employed, the number of animals used, and other conditions of the experiment.

As we have seen, he emphasizes the great part played by nutrition, and stresses also the function of "generation number" in giving a variable "helmet-potency," "spine potency," etc. At times he relegates tem-

perature to a position of insignificance, at others, as in connection with the Reactionsnorm, he seems to give it more importance. To determine the Reactionsnorm of a race there are required, he says, knowledge of its responses to low, middle, and high nourishment, at low, middle, and high temperatures and in early, middle, and late generations. To what extent are the several conclusions based upon 27 ( $3 \times 3 \times 3$ ) strictly controlled and parallel series of experiments?

Woltereck has also introduced the conception of Präinduktion referring to the indirect influence upon the young of conditions to which the mother had been subjected long prior to the formation of the eggs from which the new generation is derived.

### *Cyclomorphosis of Daphnia in Relation to Heredity and Evolution*

The genetic factors involved in cyclomorphosis are, of course, not disregarded. Heredity determines the particular pattern of cyclomorphosis displayed in a particular population (compare *b* and *c*, fig. 1). In fact it is only a modest exaggeration to say that there are as many hereditary patterns as there are waters inhabited by cyclomorphic forms. The respective winter forms of different lakes may be indistinguishable, although, if collections are made in summer, an almost infinite diversity of forms is found, each form characteristic of the lake in which it occurs. It repeats itself in successive summers and apparently, to an extent at least, in experimental cultures. Woltereck holds that the pattern is modifiable (to the eye) only after a considerable number of generations when the new pattern, a *dauermodification*, or else a *differentiation* becomes more or less definitely fixed in heredity. We need not go farther into this question now except to suggest that a promising field of investigation by experiment is indicated.

The genetic aspect of the general problem of cyclomorphosis leads naturally to the question of the origin of the multitude of summer forms. How has it come about that populations of particular lakes have in season particular forms of genetic validity—say, helmets that are upturned or downturned or directed straight ahead, long or short, rounded or pointed, etc.? We have no occasion now to go into the broad question of phylogeny, although it should be remarked that Woltereck, who probably has a wider acquaintance with limnetic *Daphnias* of the world than any one else, seems to regard both natural selection and mutation as influences of secondary importance in the origin of the several species and subspecies with their distinctive patterns of cyclomorphosis, holding rather that the environment is of controlling evolutionary effect:

"Alteration of racial qualities in daphnids is either caused or directed by certain environmental factors" (1932).

### *Other Investigations*

The work of some other investigators can be mentioned only very briefly. Langhans (1909), working with 3 non-pelagic species, *D. magna*, *pulex*, and *obtusa* and the limnetic *D. longispina*, found an inverse correlation between the accumulation of waste products (due to crowding) and both productivity and length of spine. Isolation led to greater egg production and a longer spine. Much earlier, Warren (1900) had experimental evidence that the accumulation of waste products, even in the presence of abundant food and oxygen, led to reduction of spine length for *Daphnia magna* and ultimately to general ill-health, cessation of reproduction, and finally death. Water long inhabited by *Daphnia* was injurious to fresh *Daphnia* but not to other Entomostraca—Cyclops and Cypris. In time the water purified itself without treatment and became a suitable medium for new *Daphnia*.

McClendon (1910), working with *D. pulex*, a species of only moderately pelagic habit and displaying relatively little cyclomorphosis, found nutrition the most important factor, reducing body length and the duration of development but increasing the length of the spine; high temperature, which he regarded as an adverse condition, and starvation have like biological effects. High temperature, then, had an effect in the reverse direction from that noted by others for the more strictly pelagic *Daphnias*. No effects were gained from the use of various salts in the strongest tolerable concentrations nor from the use of diverse intensities of light and darkness.

Wagler (1913), following Woltereck, related length of head to sexual periodicity. Examples taken in July, a time of reduced abundance, have shorter heads than the more numerous individuals of spring and fall. In a later work (1923) he made what seemed a most telling criticism of the temperature theory when he pointed out that the helmets are generally shorter in small ponds with relatively high temperatures while the longest helmets occur in the larger lakes with lower temperatures than those of ponds. Since he refers to the active metabolism and the excess of food in small ponds, the same argument might have been applied against the nutrition theory. Wagler emphasized stratification, a summer feature of lakes, as the significant environmental factor.

At the same time, Gruber (1923) found a direct correlation between lengths of horn and of mucro in *Scapholeberis mucronata* and the size of the body of water. *Scapholeberis* lives commonly on the underside of the surface film and therefore would not seem to be affected by stratification. It is not clear how stratification of water could act as a direct stimulus. Larger helmets were found also in geologically older waters. Gruber, then, brings in both *size of water* and *geological time* as factors in helmet development.

Schubert (1927) says that if the helmet of *D. cucullata* (very closely related to *D. longispina*) were a function of temperature, we should find the highest helmets at the highest temperatures and the lowest at the lowest temperatures, but his observations in certain lakes indicate that, although there is but one peak in the temperature curve, there may be one, two, or three in the curve representing lengths of helmet, corresponding in his opinion with the three reproductive cycles of the races in question. Therefore temperature is not the primary cause of the modification. Correspondingly, it could be argued, although Schubert does not do so, that if nutrition were the primary cause of helmet formation, the longest helmets should be found in the richest waters and, in any given water, at the time of greatest richness; but is this the case?

Wesenberg-Lund has strongly maintained his position with respect to the significance of temperature in cyclomorphosis. "The seasonal variations do not proceed evenly throughout the year, but by abrupt changes, which are accomplished in the period from the end of May to the middle of July and in Sept.-Oct.; in both cases when the temperature is ca. 14-16°C. The transition can in spring be accomplished in the course of ca. a fortnight" (Wesenberg-Lund, 1908, p. 189). It occurs simultaneously in all lakes (in Denmark) at the same temperature. Furthermore, the change occurs chiefly from generation to generation rather than during individual lives (according to variable food supply). "The outer conditions," he says, "must thus be assumed to act upon the individuals mainly during development of the embryo, less throughout growth, and least after the egg-producing stage" (1908). It is significant that there is no cyclomorphosis in northern lakes where the temperature does not rise to 16° (1910). He had first thought of seasonal variation in form as due to variation in nourishment, but abandoned the supposition because the variation in food supply could never be of such regularity as to bring about such "harmony" of change in the same lake from year to year, in all the lakes of the region and all

the different cyclomorphic organisms. Food supply might be the agent to make the change possible but not the driving force (1926). (This distinction, in connection with the preceding argument, does not seem of clear validity.)

In brief, then, where Wesenberg-Lund and Ostwald would make temperature, through its effect on viscosity of the medium, the controlling factor for change of form, Woltereck sees a double control in the external factor of condition of nutrition and the internal factor of position in the reproductive cycle (helmet potency or "labilität"), heredity, of course, giving the pattern in any case. It is the contention of the adherents of Woltereck's view that, if temperature were the controlling factor, the greatest helmets should be in the warmest waters, which is not the case. On the other hand it is the equally valid objection of Wesenberg-Lund (1926) that if nourishment were the primary regulator, the greatest helmets should be found where the food is richest, which, he says, is not the case. Wesenberg-Lund also questions the correlation of stratified food supply and helmet development, which seems to be an important part of the theoretical base of Woltereck's explanation of the origin of helmets. We are dealing with a phenomenon that manifests itself most conspicuously in the open areas of lakes where the waters are relatively cool and the food may be relatively scant. In ponds where the waters become very warm and the food may be very abundant—it is precisely in such waters that cyclomorphosis does not occur in any prominent way. The novice might assume, then, that there is no controlling factor, or that, if there is, it has not yet been pointed out.

Yet, as Wesenberg-Lund says with respect to the bodies of water in which cyclomorphosis manifests itself: when the water warms up the helmets and extensions appear, and when the water cools off they disappear; this, if it be a general rule, must have some meaning.

In our experiments we have attempted to see what changes in form could be effected by mere change of temperature, and we have made use of an animal that displays a seasonal change of form, not so radical as that of *D. cucullata*, but yet quite marked. Our animal has a special advantage for experimental work, in that the extension of the head characteristic of the summer form is a *positive* acquisition. Mathematical measurements are helpful in respect to the degree of its development or in conveying information to others, but one can tell at a glance if the point is present (however small) or absent (see fig. 4, second row, and fig. 7).

## II. OBSERVATIONS AND EXPERIMENTS

*The Animal in Nature*

Our material was derived from a relatively new artificial lake formed near Chapel Hill, N. C., by the repression of three streams just below their junction. The lake is narrow, its several arms one to one and a half miles in length, but not exceeding a quarter of a mile in width, the area only some 200 acres, the depth near the dam, where all our collections were made, about 20 feet. The lake is distinctly immature, having been formed in 1932. The predominant plankters are *Daphnia longispina*, *D. pulex*, *Cyclops leuckarti*, *C. prasinus* (?), and the rotifers *Notholca* and *Conochilus*. Calanoid copepods have not yet appeared. The *Daphnia* studied and employed in the experiments is provisionally

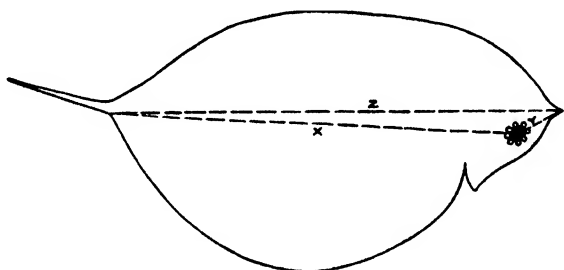


FIG. 3. Showing mode of measurement; see text below

called *D. longispina*. Being without an ocellus it should perhaps be called *longiremis*, but it is at least of the *D. longispina galeata* series belonging to the group of species or subspecies of which *cucullata* forms the terminal series.

For each set of measurements 50 animals of medium size (.70 mm.  $\pm .08$  mm.), taken at random, were sketched in outline with camera lucida and measurements made on the sketch from the center of the eye to the front of the head (Y) and from the center of the eye to the base of the spine (X) (fig. 3).

In a collection of January 24th, 1934, all examples were round-headed (fig. 4) as is regularly the case in winter (from observations at various times during five winters), and the quotient of  $\frac{Y}{X}$  was 0.10. *Daphnia* were then scarce, constituting only 8 per cent., by number, of the net zooplankton. On April 5th, *Daphnia* were more abundant, representing 82 per cent. of the net zooplankton and occurring in both round-head

and pointed-head forms (fig. 4, second row), the latter predominating in the ratio 44:38. The quotient of  $\frac{Y}{X}$  for round heads was again 0.10

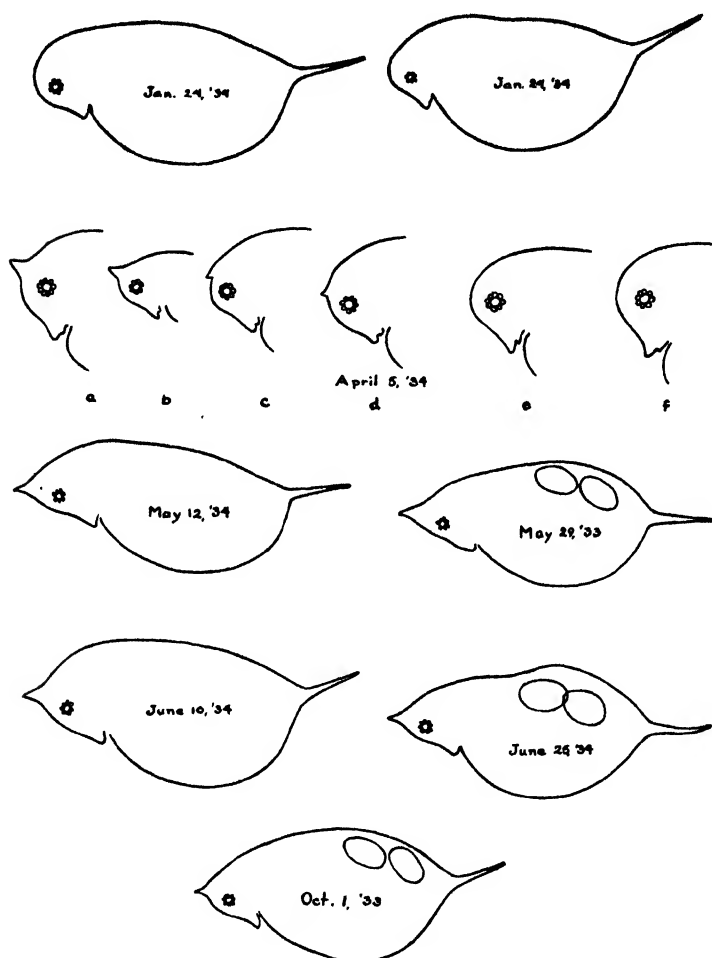


FIG. 4. Illustrating cyclomorphosis of *Daphnia longispina* in University Lake, Chapel Hill, N. C.

and that for pointed heads was 0.144. On May 12th, and thereafter, only pointed heads were found (fig. 4, third row). The quotient of  $\frac{Y}{X}$

May 12th was 0.209, showing a much greater development of the point than was found early in April. A collection made in May of the preceding year gave a generally similar result with  $\frac{Y}{X} = 0.18$ . Three collections in June made on the 10th, 23rd, and 25th (fig. 4, fourth row) gave quotients of 0.192, 0.191 and 0.199, respectively. Larger examples have the helmet relatively less well-developed (fig. 5).

It is evident, then, that the extension of the head before the eye is practically doubled in late spring as compared with the condition in

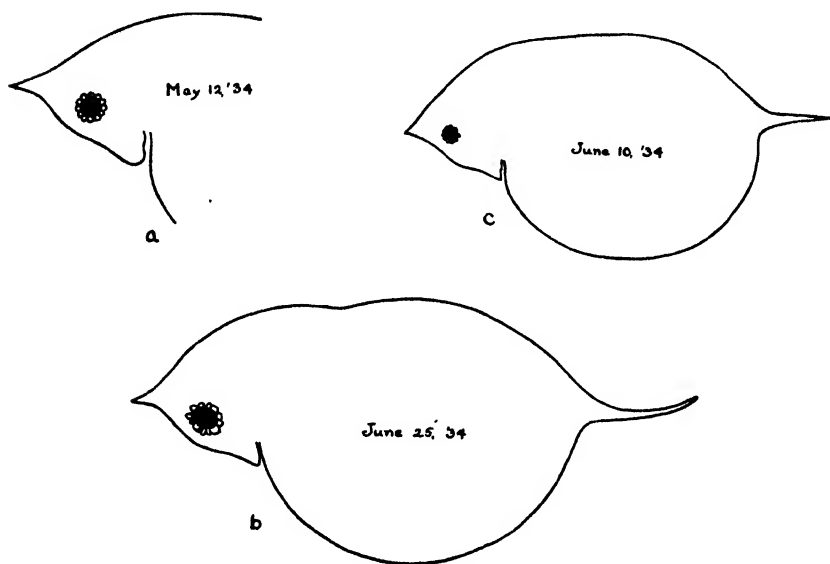


FIG. 5. Showing extreme helmet development (a); older *Daphnia* may retain pronounced helmet (b); but generally have shorter ones (c).

January, but there is no increase in length of helmet in early summer. Since a collection made on October 1st of the preceding year included *Daphnia* with strongly pointed heads (fig. 4, bottom), the quotient  $\frac{Y}{X} = 0.185$ , and round-headed *Daphnia* were found a little later, there seemed to be a definite cycle, which could be stated as follows: In winter only round heads; in late spring and early summer only strongly pointed heads until disappearance of the species; in early spring and fall both types occurring together, with the points in spring not appearing in



fullest development until late in the season. Such a rule would commend itself for simplicity and for conformity with the facts during one year. It does not, however, conform exactly with the facts of suc-

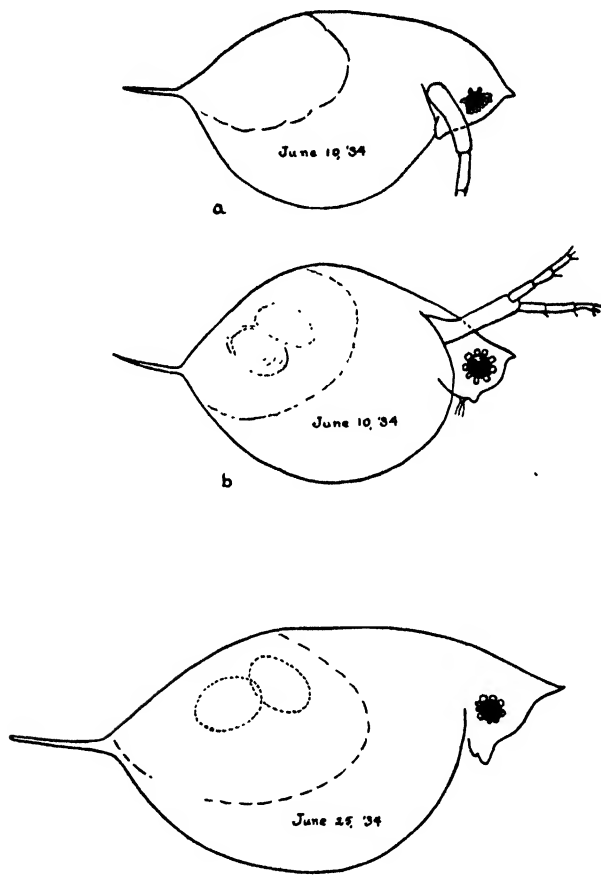


FIG. 6. Stages in development of ephippia, University Lake, June, 1934. The particular animals, especially *b*, are evidently in bad condition; such animals are very rare in the lake and have never occurred in cultures.

ceeding years. During 5 successive Januaries, there have been found only round heads, and the species seems always to disappear or become very rare in midsummer—how or why we do not know since ephippial females (fig. 6) have been found but rarely and about as frequently in

November as in June. In the autumns of 1934, 1935, 1936, and 1937 (in contrast to the condition in 1933) pointed heads were very rare, and particularly so in the early collections when the water was still relatively warm—up to 20°C. or more. Furthermore, in 1935 about two-thirds of the *Daphnias* were helmeted by March 29th, but a fair proportion of round heads persisted as long as there were *Daphnias* in the plankton or up to the end of June.

The rule as to seasonal polymorphism is, therefore, only a rough approximation. The correlation with temperature has failed in early fall in every year but one, and it failed partially in the late spring and early summer of 1935. It will appear later that there are difficulties in reconciling the results of experiments in the laboratory with the results of observations on collections in the lake.<sup>3</sup> Hardly a better illustration could be found of the necessity of checking results gained in the laboratory against observations in the field.

### *The Animal Under Conditions of Experiment*

#### Materials and Methods

The experiments conducted with *Daphnia* derived originally from the lake were comprised chiefly in 5 series: (1) Addlestone's "straight-temperature," (2) his "transfer" experiments (1934), (3) Coker's straight temperature, and (4) his transfer experiments (1935), and (6) Taylor's straight temperature experiments (1936). The straight temperature experiments were those in which the parthenogenetic animal was kept under a fixed or relatively fixed temperature during at least the whole period of incubation of a clutch of eggs. The transfer experiments were those in which the animal was transferred from one temperature chamber to another so that developing eggs or young were subjected to different temperatures at different times during the period of development. Coker's experimental lines (chiefly three: Nos. 6, 8, and 14) were derived from round-head parthenogenetic females collected in January; Addlestone's and Taylor's from a laboratory stock originally derived from animals collected in the fall—the original females having pointed heads in Taylor's case, uncertain in Addlestone's. Since ephippial females have rarely been found, stem mothers could not be used.

The cultural methods employed by the senior author are described; those of the others were essentially the same, except that in Taylor's

<sup>3</sup> Miss Patty Hill assisted in study of the material from the lake.

experiments overfeeding was deliberately practiced but with generally deleterious results. Mass cultures were never employed; more impressive numbers could be obtained by their use, but only with an undesired complication of environmental factors through accumulation of waste products and in other ways.

Parthenogenetic females, or young, were isolated in shell vials (or in a few cases in large vessels) provided with culture medium made up of filtered aquarium water (rarely of filtered lake water), to which was added a few drops from a protozoan culture and an alga culture (generally *Ankistrodesmus*). The protozoan cultures were derived in the following way. Several quart jars of stock culture were regularly on hand, made up by filling the jars about one-fourth full of dried horse manure or sheep manure and adding filtered aquarium water to near the top. The culture ripened in a few days. Every few days each of these was examined to select the one that contained the most nearly pure culture of minute protozoa—*Chilomonas* or other protozoa of small size. It has been observed that large infusoria, such as *Paramoecium*, clog the filtering apparatus of *D. longispina*, causing a temporary interruption of the feeding process while the large infusorian is "kicked out." With a pure culture of *Chilomonas* a continuous stream of food may be observed to pass into and along the alimentary tract of a *Daphnia* lying on its side in a drop on the slide. The mandibles of *D. longispina* have good teeth, but for what purpose they are used has not been observed.

The stock culture for use having been selected, a quantity of the medium was passed through medium fine filter paper into a 100 cc. bottle to which was then added a pipette or two of the pure cultures of algae; the filter eliminated debris, and most of the larger protozoa. Feeding was done from the best of the filtered media, several of which were always at hand. One might be good for a day only; another would continue productive for several days.

When young were born each was placed in a separate drop on a slide and examined under the microscope for form of head. Each one to be used for breeding purposes was then placed in a shell vial to itself with about 20 cc. of filtered aquarium water to which was added enough of the food culture (2-10 cc.) to give a slight cloudiness to the water. Examination and feeding was done every day at 20°, every other day or oftener at 12° to 16°, and at least every third or fourth day at 9°. From the record kept for each culture, birth could usually be anticipated within a day and supplemental examinations made accordingly. About once a week, or a little less frequently at lower temperatures, the entire medium in a culture vial was changed.

We did not attempt to control all conditions of the experiment—food, oxygen, carbon dioxide, etc. What we did was to keep the one influence, *temperature*, under control (roughly in first experiments, more precisely in the later ones), letting the other possible sources of influence (except light and size of container) be moderately variable, and then to check the consistency of the results as the experimental factor was changed.

### *Experiments with "Straight" Temperature*

When the first series of experiments were conducted by Addlestone in 1934, apparatus permitting accurate temperature control was not available. The following temperature conditions were utilized: (1) A cold room used for other purposes, in which the temperature was generally 4-5° but occasionally a degree higher or lower; (2) a water bath with running tap-water, its temperature at first fluctuating between 8° and 13°, but rising in the latter part of the season to 16° (no individual experiment was, however, subjected to a range of more than 4 or 5°); (3) a basement room in which the temperature fluctuated from 18 to 23°, and rarely to 25°; (4) an oven with temperature nearly constant at 28°. At each place temperature was recorded three times daily.

Since all *Daphnias* reared, whether born with round or pointed heads, became round-headed in course of development, and, in every case, except two, before attaining sexual maturity, we may refer for the present only to the *form of the head at birth*. In the cold room (5° ± C.) 31 round-head young were liberated; in the water bath in the early part of the experimental work (8°-13°C. and generally below 13°) 100 round heads and no pointed heads appeared; in the basement room (20° ± C.) 160 pointed heads, and in the oven (28°C.) 61 pointed-head young were liberated. Thus we have 131 round-head young at low temperatures (below 14°C.) and 221 pointed heads at high temperatures (about 18°C.). In many instances (11 at least), the same parent was allowed to produce young at low and high temperatures in alternation, but the form of the head in the young corresponded without exception to the temperature rule just indicated. There were, however, 4 broods, in addition to those mentioned, in which both forms of heads appeared, and these were born at temperatures of about 14° or above, but well below 18°.

The following tentative conclusion seemed justified: The form of the head of the young is subject to control by regulation of temperature and the critical temperature is somewhere in the vicinity of 14°, at least between 12° and 18°C.

It was desirable, of course, to have more precise control of temperatures below room temperature, but we did not find on the market an apparatus of sufficient flexibility and convenience of form. With the aid of Dr. E. W. Constable, a new apparatus was devised to give precise and continuing control to a tenth of a degree at any desired temperature and permit several temperatures to be maintained simultaneously (Coker and Constable, 1936). Another series of experiments was then conducted by the senior author with results on the point in question as given in Table I.

These results conform with those of the preceding series of experiments as to the general level of the critical temperature for change of head

TABLE I

*Numbers of Daphnia longispina born at several constant temperatures and percentage with pointed heads at birth*

TEMPERATURE <sup>4</sup>	TOTAL NO. BORN	NO. WITH ROUND HEADS	NO. WITH POINTED HEADS	PERCENTAGE WITH POINTED HEADS
°C.				
9	58	58	0	0
11	196	194	2	1
12	116	99	17	14.7
13	75	50	25	33.3
14	55	7	48	87.3
16	32	0	32	100.0
20	101	0	101	100.0
	633	408	225	

<sup>4</sup> For present purposes, temperatures are stated in even figures. That in some experiments the bath may have been set at 0.1° or 0.2° above or below the even figure is immaterial in this discussion.

form. They show, however, that there is not a sharply defined critical point on the temperature scale, applicable to all breeders or young, but rather that, under the conditions of the experiments, the critical temperature varied between 11° and somewhere below 16°. Subsequently Taylor, in connection with experiments having a different objective, observed 45 young born at 21.6° and 60 born at 15.1°, all with pointed heads and 11 born at 11.1° with round heads. The critical range is narrowed from 11° to 15°, centering apparently, at a little above 13°.

Conditions of food supply may have had some effect in shifting the apparent critical temperature in some cases in one direction or the other, but it seems highly improbable that three different experimenters, in

three different years, with a number of different stock food supplies, should have attained results in such close correspondence with respect to the same experimental variable, if that common variable (temperature) were not a highly significant one. In fact, in connection with other studies, many other *Daphnia* have been bred in the laboratory at temperatures sometimes below and sometimes above the critical range, and exceptions to the rule simply do not occur.

It may be recalled that breeders were kept in individual vessels, abundantly fed, and protected from excessive accumulation of waste products. It is to be noted here that Wesenberg-Lund (1926), after many years of observations in the field, found that the change of form of wild *Daphnia cucullata* in lakes of Denmark occurred in early summer, soon after the temperature of the water rose to about 12–16°C.



FIG. 7. Illustrating least development of helmet as "bump," "angle," or hook. Contours of brow of *Daphnia* bred at 12°C., although round heads are the rule at this temperature.

Since we find both pointed and round heads appearing at temperatures within what may be called the critical range, it may be of interest to examine more closely the broods reared at 12°, 13°, and 14°C. in the second series of experiments where temperatures were precisely controlled throughout the course of each experiment.

The 23 clutches of 3 lines born at 12° were either all round heads or mixed, embracing some with clearly rounded heads, some with slight but distinct points, and some with mere bumps (fig. 7). Only a single clutch had no round heads, and that comprised but one individual with small point. Not one animal in any of these clutches had marked points. At 13° mixed broods predominated (9 out of 15) and 3 comprised exclusively pointed heads. At 14°, 13 of 18 clutches were made up exclusively of pointed-head young in which the points might be very

insignificant or sometimes quite large; there were only 3 mixed clutches and 2 having 1 round head each. In the mixed clutches at 13° and 14°, and in the purely pointed-head clutches at 13°, the points were all very small and sometimes mere "bumps." Even at 16° (11 clutches), about half of the points were small, whereas at 20°, only 6 of 101 points were described as "small" (but not insignificant), while most of them were very pronounced.

There was no evidence from rate of growth or size of broods to indicate that deficiency of food was associated with roundness of head. In fact, the average number of young in the clutches was notably greater at lower than at higher temperatures, being 8.3 at 9°, a little over 5.4 at 11°, 5 at 12° and 13°, 3 at 14° and 16°, and 4 at 20°.° The numbers are not now considered significant except in a negative way, as offering no evidence of superior nutritive conditions where extension of the head characterized the newborn.

With respect to the 3 lines employed in Coker's experiments, there was apparently not half a degree of difference in the responses of the several lines to temperature.

### *Transfer Experiments*

These experiments were made to determine the effect on the developing eggs or embryos of a change of temperature during the period of development. Addlestone made 27 transfers of parthenogenetic females (15) from one temperature to another involving 30 clutches born under conditions of transfer, besides 15 born before transfers. In all 97 young were born after transfer. In 14 cases (44 young) where the eggs were passed into the brood pouch after the transfer, there was no evidence at all of an influence of the original temperature on the form of the young; 12 cases (41 young) where the transfer was made late in the incubation period the young had clearly the form corresponding to the second temperature. The exact critical period in incubation was not discovered.

In another series of experiments the senior author made 35 effective transfers of females with young in the brood pouch. (A good many transfers are ineffective, because the young are not infrequently aborted and lost with severe change of temperature.) The following landmarks in development were noted:

<sup>5</sup> Contrary to Ostwald's view that low productivity with low temperature is the rule.

- (1) New eggs in brood pouch
- (2) Eggs hatched (the shells are cast early in development)
- (3) Head outlined
- (4) Advanced embryos with appendages showing
- (5) Two-eyed embryos
- (6) One-eyed embryos
- (7) Young liberated ("born")

In general the results from all transfers, with a total yield of 195 young, correspond to the rule that the new temperature is ineffective as to form of head after the distinct appearance of the two eyes, whether the transfer was from a lower temperature to a higher or the reverse. There were, however, a few exceptions that may be significant. In two cases of transfer from 16° to 13°, with "hatched eggs" in the brood pouch, when the expected form would have been that of 13° (with no points or with only insignificant ones), 2 of 7 and 4 of 5 young had notably larger points. In a 9°-20° transfer, 2 young moved to the chamber of higher temperature before the appearance of eyes, had round head and "angled" head, respectively, instead of pronounced points. A female with "hatched eggs" transferred from 12° to 20°, yielded 3 young with small instead of large points. Probably the most notable exception was a clutch of 5 young born at 20° after transfer in the stage "head outlined:" 1 of these had a round head, and 4 only tiny points or angles, where prominent points might be expected.

Two clear exceptions and 14 partial ones do not constitute an impressive number of exceptions, but these do suggest that there is an influence of temperature during the early part of development, which is usually, but not invariably, overruled by the influence of the conditions surrounding the embryo during intermediate stages of development. It may be remarked that Ostwald (1904), from two chance observations of gravid parents transferred from the room to the cold bath at 3 and 4 days, respectively, before liberation of the young, when the young in the first case had somewhat longer heads than the mother and those in the second case had somewhat rounder heads, concluded that the form-determining influence of temperature takes effect only between the third and fourth day of development, or at the beginning of the second half of the period of incubation. The evidence was meagre and might have been interpreted more logically as indicating that temperature ceases to exert an effective influence after a certain critical stage. He was nevertheless correct in suggesting that with respect to the influence of temperature there was a critical stage in embryological



development which could be determined more accurately only by further experimentation. Our observations suggest that the critical stage *beyond which temperature is ineffective* is somewhat variable but generally at the stage marked by the appearance of the 2 primitive naupliar eyes.

Finally, it may be noted that the transfer experiments confirm the straight temperature experiments as to the influence of temperature on form of the newborn, merely fixing more definitely the time of action as being after the eggs are in the brood pouch and before a certain stage in embryonic development has been attained. The 195 young bred in these experiments may, therefore, be added to the 1116 reported in preceding paragraphs, making the total young liberated at various temperatures 1311 (besides others not here listed) without a single clear exception to the inferred rule of correlation of form of newborn with temperature; the few exceptions to the "rule" as to critical period in development are not, seemingly, exceptions to the general rule of correlation.

There seems, then, to be a definite influence of temperature, as it acts on the animal itself and not upon its food supply. It may be said, of course, that it is the effect of temperature on the assimilation capacity of the animal, but this, after all, is a direct effect on the animal. Neither Wesenberg-Lund nor Ostwald have suggested that temperature acts, directly or indirectly, except through an influence on the metabolic activity of protoplasm. The influence on the young might, however, be direct (in this sense) or it might be indirect through the mother, which under different conditions of temperature could contribute to the developing eggs or embryos different quantities or qualities of nourishment in consequence of changes in her own metabolic activities. Let us now examine this question.

All of the experiments indicate that prolonged subjection of a female to either low or high temperature has no appreciable effect on eggs laid at a new temperature as regards the form of the head of the young hatched from them. There is no Präinduction in the sense of Woltreck, as regards form of head at birth. It seems clear that the influence is exercised chiefly during intermediate stages of development of the embryo.<sup>6</sup> It might still be that the embryos are affected, not directly

<sup>6</sup> It is assumed by some investigators that temperature, or some other condition, is effective only when it leads to the formation of a helmet. Unless there is a fallacy in our reasoning, the round head is as much a product of the interaction of internal and external factors as is the pointed head; low temperatures may be as positive in action as high temperatures.

by the temperature, but by something furnished by the mother as a secretion from the lining of the brood pouch. For more than half a century the brood pouch of Cladocera in general has been commonly assumed to be a sort of uterus into which the mother secretes necessary nutritive substances; but Rammner (1933) finds that with several species of *Daphnia* and *Simocephalus*, the eggs develop just as well if removed from the brood pouch in a very early stage of development, even before they are hatched; in *Moina*, *Leptodora*, etc., the case is different—the pouch is a uterus. During the past year I. S. H. Metcalf, a student in our laboratory, succeeded in having a small number of new eggs that had been removed from the brood pouch complete their development in depression slides or hanging drop cultures. The form of the head at the stage of normal “birth” corresponded with the temperature at which the eggs were kept regardless of the temperature to which the mother had been subjected while the eggs were being formed and extruded into the brood pouch. Exclusive of cases where the temperature of artificial incubation was the same as the temperature at which the eggs had been formed in the mother: there were 9 taken from mothers at 10.2° and incubated at 19.05°—all had pointed heads; there were 3 taken from others at 19.05° and incubated at 10.2°—these developed round heads. One clutch of 7 eggs formed by a mother at 10.2° was divided into two lots: 4 eggs were incubated at 10.2° and 3 at 19.05°; the former developed round heads, the latter pointed heads.

There is clearly no need now to make any other inference than that temperature, acting directly upon the embryos, exerts some influence on growth or multiplication of cells to cause the production of helmets, or points, at temperatures above a critical level that lies around 13°C. (or about a couple of degrees lower or higher with different individuals).

Before, however, we become too strongly impressed with the significance of temperature in the regulation of the form of the head, the facts presented in the next section must be considered.

#### *Loss of Point after Birth*

We have noted that temperature seemed to lose its power to influence form after the appearance of eyes in the embryo. This seeming loss of influence may be actual or it may be that there is not time after the eyed stage and before birth for the influence to exert an observable effect. Now it happens that, with all the pointed-head young reared in the experiments of Addlestone and Coker, the point was invariably lost in course of the first few molts; once lost, it was never regained. Therefore, all breeding animals (except 2) were round-head, regardless of the

temperature at which they were born or bred, and the two exceptions, retaining a vestige of a point at the primipara stage (3rd to 5th instar), lost it in the next succeeding molts.

In the experiments of Taylor the loss of point occurred in a similar way, except that in 5 of 29 reared at 15.1° and in 1 reared at 11.1° (but bred at 15.1°) the point, although reduced by the 3rd or 4th instar to a vestige, was never lost. Furthermore, in 18 of those reared at 15.1° and in 5 reared at 11.1° (but bred at 15.1°) a good point subsequently developed, and in six others at 15.1° a slight hook or an angle appeared. The development of the point during free life cannot well be attributed to temperature but evidence as to the actual cause is wanting. One can only think of something in the surrounding medium. Miss Taylor's animals were, by the way, reared in larger containers. Certainly, in the wild state in the lake the points are not lost, but round-headed *Daphnia* are either wanting or relatively few during late spring and early summer, a period of great reproductive activity.

As Wesenberg-Lund has pointed out, it is difficult to reproduce in small vessels in the laboratory the conditions to which a pelagic animal is accustomed. We have had the same experience as some others in this—that the majority of wild *Daphnia* die when brought into the laboratory. Once, however, a line has been established, our *Daphnia longispina* have showed a most satisfactory adaptation to our cultural conditions. Fertility and viability have improved with succeeding generations. Sixty days or more was not an uncommon duration of life: the maximum was 88 days and some might have lived longer but for the termination of the experiments. The number of clutches from one female varied from 1 to 8. The numbers of young per clutch, although always small 1 or (2) with the primiparae, was with older breeders often 10 and occasionally 13 or 14. The number of generations in a line (7, the maximum) was limited only by the duration of the experiments. Evidence of lack of adaptation might be found in the fact that sometimes an individual would go for a long time without extrusion of eggs, when one or two complete changes of medium would be followed by active egg-production. Never, however, in such cases, did the form of the head of the young born from such eggs reveal any influence of conditions other than temperature. Never also was there evidence of "Depression" in production of males or ephippial females.

The possible influence of *light* is of course to be thought of. In the senior author's experiments all culture vessels were in the dark, so that light could not have been a factor in producing the change from round to pointed heads.

*Generation Number and Präinduction*

Woltereck reports a remarkable difference in the responses of *D. cucullata* to external conditions in the first and sixth generations (fig. 2). Our experiments offer no support to that view. The negative evidence of our experiments on this question may perhaps be subject to some discount, since we bred only 7 generations from a wild generation of unknown number. Nevertheless, the regularity with which the form of the head of the newborn in a number of series of experiments (including several not mentioned here) is found to conform to a rule of correlation of head-form and temperature during incubation makes it seem quite unlikely that the place of the individual in the hypothetical reproduction cycle has anything to do with the response. Furthermore, evidence gained by several investigators previously cited tends to discredit the significance and even the existence of a "reproductive cycle."

In the lake, the last parthenogenetic generation certainly shows no loss in capacity to form helmets (see fig. 6 c where  $\frac{Y}{X} = 0.22$ ); and that, notwithstanding the fact that some of the animals show signs of "Depression."

As to Präinduction, or the effect on the *germ cells* of the embryo in the brood pouch of the mother, carrying the hypothetical control back one complete generation, our evidence is decidedly on the side of the negative.

*Comment*

So extraordinarily complex are the form relations of pelagic *Daphnia*, where every lake seems to have its own particular race, as Wesenberg-Lund and Woltereck have found (notwithstanding that change of form in spring, and sometimes in fall, synchronizes roughly at least with temperature), that it would seem foolhardy to attempt now to apply any simple explanation to the whole phenomena of cyclomorphosis. Wesenberg-Lund (1926) describes a race of *D. longispina galeata* in which the young at all seasons are born with round heads, while the mature animals show a marked elongation of the head in summer; and another in which both round and pointed heads occur in winter (and this in Denmark) but the points are high and sharp only in summer. Again he compares two races of *cucullata* from waters less than half a kilometer apart, a lake and a pond with insignificant difference of temperature. In the lake a marked cyclomorphosis extends through the summer; in the pond a dwarfed but heavy race begins a cyclomorphosis

in June, but in July the crest diminishes until typical round heads appear in August. In midsummer there is a maximum of numbers in the lake and a minimum in the pond; this suggests that nutrition could be a factor, but Wesenberg-Lund thinks it highly improbable that the dwarf race is a result of starvation, although he says there must be something with respect to assimilation to cause the decrease in length, in crest, and in numbers for the race in the pond, just when the race in the lake attains its maximum in all these respects. In both waters the number of eggs per clutch is reduced at this time to 1 or 2, which does not suggest a strong contrast in nutritive conditions.

From field observations, Wagler (1923) suggested that the high temperature and abundant food-supply of ponds promotes rapid development, maturity at small size, and small crests, and the lower temperature and poorer nourishment of lakes, a slower development, larger size and higher crests. He recognized that this seemed to conflict with the experimental data, but suggested no means of reconciliation. His suggestion does not appear, either, to fit the sequence of events in a given lake.

It seems impossible to escape the conclusion that, under the conditions of our laboratory experiments, temperature controls the form of the head of the newborn,<sup>7</sup> but does not control that of the free-living. In the lake temperature does not constitute a sufficient explanation, but is probably involved. In both cases it is probably temperature *plus*. In another paper (1939?) we have discussed the "plus" factor which may be a positive (promotive) or a negative (inhibitory) one. Without repeating that discussion, we may allude here to the results previously obtained by Warren and Langhans and cited p. 52 above. These data do not, however, offer a good parallel to our results, since in our cultures the loss of helmets was unaccompanied by detectable signs of

<sup>7</sup> It may not have a direct bearing, but the work of H. R. Seiwel (1930) in our laboratory on the heart-beat of a related Cladoceran, *Simocephalus vetulus*, ought not to be overlooked in this connection. In that study it seemed clear that there was a "critical temperature" for rate of action of the heart in the neighborhood of 13°. The heart of *Simocephalus* and the form of the head of *Daphnia* are not the same thing, but the two animals are very closely related, originally of the same genus. Between 12° and 14° something happens in *Simocephalus* to cause a notable change in the response of the protoplasm of the heart to conditions of temperature; between 12° and 14° something happens in *Daphnia* in the protoplasm of head-forming cells to effect a notable change in the response to temperature as respects the relative rates of growth or multiplication. There may be something in the idea of a critical temperature for Cladocera at about 13°.

ill health or loss of reproductive capacity but rather, generally, by a naturally growing reproductive efficiency.

Finally it should be emphasized that the experimental conditions have not given us any form of head that is not in character with forms displayed by the wild *Daphnia*. We have obtained head forms in considerable diversity but all conform to the genetic pattern. Experimental conditions determine only the appearance or non-appearance and the degree of development of a structure the general nature of which is fixed by heredity. We get smaller or larger University Lake helmets, or no helmets, but never, for example, a Chautauqua Lake helmet (contrast fig. 1c with all other figures).

The problem is complex, as might be expected. We have attempted an experimental attack on one phase of the problem, and the following conclusions seem justified.

#### CONCLUSIONS

1. The form of the head of the race of *Daphnia longispina* in University Lake shows seasonal variation, only round heads appearing in winter and chiefly prominently pointed heads on young and old in late spring and early summer. Mixed populations of round and pointed heads are present in early spring and in mid-autumn. At first in spring the points are small, but, so far as we have observed, the fullest development of the head is attained by early May and no further expansion occurs thereafter. A strict correlation with season or with temperature seems to fail, since some round heads have been found in June and a whole population of round heads in September, when the water is quite warm.

2. In the laboratory the critical temperature for form of head of the newborn is about 13°C., but developing young subjected at a proper time during incubation to a temperature a degree or two above or below 13° may have round heads or heads with minute points or angles. At temperatures below 11° only round heads, and above 15° only pointed heads are developed. Young incubated at 16° have marked points, at 20° usually much more prominent points.

3. The form of the head, pointed or rounded, of newborn in the laboratory is determined by the temperature to which they are subjected during intermediate stages of development. Change of temperature after the 2-eyed stage has ordinarily no effect on form of head. Possibly the effect of temperature may be cumulative during the early and middle period of development, for there is slight evidence that conditions of

temperature during the early part of the period of incubation have some effect. Presumably temperature acts through an influence on the metabolism of the developing embryo.

4. A few eggs incubated without the brood pouch developed into young with form of head corresponding to the temperature of incubation, not to that to which the parent had been exposed.

5. As a corollary to conclusion (3) with some corroboration in (4), the temperature to which the parent is subjected during the formation of eggs in the germarium, or at any time except during the first two-thirds of the period of incubation, has no effect on the head of the newborn; the conditions to which the grandparent was exposed have no effect: there is no "Präinduction" as regards the form of the head at birth.

6. The evidence as respects abundance of food supply on form of head of newborn is entirely negative.

7. There was no detectable influence of temperature on the form of the head of young in the free-swimming state or on that of sexually mature females.

8. Young born with pointed heads have invariably lost, or almost lost, the point in course of the first few molts, but in a few instances the points have been regained at about the primipara stage (3°-5° instar). Conditions governing loss and recovery of point have not been determined, but it is evident that temperature is not the primary factor. Since Daphnias in the lake at the proper seasons have conspicuous points at all stages, the loss of point in the laboratory must be attributed to some deficiency in the cultural medium.

9. Although at times unfavorable experimental conditions were indicated by the more or less prolonged interruption of reproductive activity, by the formation of imperfect eggs or by the loss of spines, such occasional and supposedly "depressive" conditions never led to gamic reproduction or to change in the relation of form of head of the newborn to temperature. That the experimental conditions were generally favorable is indicated by low mortality, generally long life, frequent extrusion of eggs, and large clutches from older animals.

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# ANOMALIES OF CRUSTACEAN DISTRIBUTION IN THE CAROLINAS WITH LIST OF CYCLOPOIDS OF THE GENERAL REGION OF CHAPEL HILL, N. C.

By R. E. COKER

WITH 16 TEXT FIGURES

Studies of the fresh-water plankton Crustacea and decapod Crustacea in the southeastern states are very restricted, with the consequences, not only that the crustacean fauna of the region is little known, but also that general accounts of crustacean species and their distribution in the United States are quite imperfect and even, in many cases, decidedly erroneous. It is intended to record here a few observations of more than usual interest, most of which have been made by chance and incidental to other studies.

## CALANOID COPEPODS

In another place (Coker, 1938?) we have discussed the crustacean fauna of White Lake, in Bladen County, N. C., with its calanoid, harpacticoid, and cyclopoid copepods appearing far from previously known ranges for the several species or groups of species (*Diaptomus minutus* Lilljeborg, *Epischura nordenskioldi* Lilljeborg, *Cyclops nanus* Sars, *Bryocamptus australis* mihi, *Attheyella wierzejskii* (Mrázek)).

Until *Diaptomus birgei* was taken in Lake James, N. C. (Coker, 1926), Marsh, who was the best authority on American centropagids, regarded that species as distinctly northern and unlikely to be found south of 39°N. latitude, or, say, the latitude of Washington, D. C. (Marsh, 1907). Having found this species as the only calanoid occurring abundantly in Durham City Reservoir, Lake Michie near Durham, and Brant Lake near Greensboro, we suspect now that it is the most common fresh-water calanoid of central North Carolina.

The finding of *Diaptomus reighardi* Marsh in Lake Mattamuskeet, Hyde County, North Carolina, collected by Dr. S. F. Hildebrand near New Holland, N. C., May 8, 1935, and recently identified by Dr. S. F. Light, offers another case of notable extension of range, since the species has hereto been recorded only from the near vicinity of the Great Lakes.

Concerning *Diaptomus augustaensis* Turner, an example of which I collected near Chapel Hill in a bayou off Bolin's Creek, Marsh remarked that it was the only specimen that had ever come to his attention. The bayou has subsequently been destroyed by drainage operations of the municipal sanitary service. This species was previously known only from the type locality, Augusta, Ga., where it was collected and described by Turner (1910). *Osphranticum labronectum* Forbes has been found in the same bayou, as well as in pools across Bolin's Creek from Glen Burnie Farm, in a marsh at the Mason Farm (all near Chapel Hill) and in the impounded Golf Creek near Pittsboro, N. C. Although it is known from Oregon to Washington, D. C., and from Minnesota to Alabama, Louisiana, and Guatemala (Marsh, 1933), the infrequency of its discovery and the irregularity of its known distribution make any local record of significance.

#### HARPACTICOID COPEPODS

Harpacticoid records in my papers of 1934 and 1938 (?) give great extension of range for several species, including some alleged "glacial relict" types.

#### CYCLOPOID COPEPODS

Species of cyclopoid copepods, as is well known, have such general distribution, world-wide in some instances, that we need single out here for special mention only two of the sixteen or more species found at Chapel Hill. Others are listed at the end of the paper.

Until this year *Cyclops nanus* Sars, found in weeds on the bottom of White Lake, seems to have been unknown in this hemisphere (Coker, 1938?).

Several years ago, a very small but crassly built copepod identified as *C. crassicaudis* Sars, then known only from Europe, was found in a wheel rut in a wagon road passing through a pine woods *on the top of a hill* just south of the present Kenan Stadium. First collected by L. L. Hill, when a student in our laboratory, it reappeared in the same wheel rut year after year. Meantime the species has been recorded from other places in the Western Hemisphere (from New York—Kiefer, 1927; and from Canada—Wiley, 1929). Since almost any species of cyclopoid may be expected to be encountered anywhere in the world, the anomaly of the present record derives chiefly from the repeated (up to 1937) and seemingly exclusive local occurrence of this rare species in a temporary water on the very top of a hill; but in Europe also the species

usually occurs in very small temporary waters. As Kiefer has suggested, it is quite possible that the species would be more widely discovered in America if sufficient search were made in the proper sort of places. The identity of *crassicaudis* is not easily mistaken. I know of no other copepod having the peculiarly crossed spines (figs. 9, 10) on the end of the endopod of the fourth foot of the male (Kiefer, 1928, p. 245, Hill and Coker, 1930, p. 216); in what appear to be atypical forms, or subspecies, there is in this place an inner seta and an outer spine (also crossed) (Kiefer, 1928; Gurney, 1933). (Length of our females: 0.58–0.77 mm.)

#### CLADOCERA

Many species of Cladocera, like some cyclopoid copepods, are seemingly of world-wide distribution, but the aberrant *Holopedium* (of the very small family Holopedidae), with its large gelatinous case and single-branched antennae (of the female) is not one of these. The better known species, *Holopedium gibberum* Zaddach, has been found generally in northern waters relatively free from mineral salts, such as mountain lakes in regions of igneous rock. In Europe its distribution indicates a preference for distinctly acid waters of pH 4.5–6 (Tauson, 1932). In America it has been found in middle northern and northwestern lakes. A related species, *amazonicum* Stingelin, has been described from near the mouth of the Amazon and reported also from Lake Charles, La. I have found no previous record of either species in southeastern states;

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FIGS. 1–13. *CYCLOPS CRASSICAUDIS* G. O. SARS, REGION OF CHAPEL HILL, N. C.

Fig. 1. Dorsal aspect of mature female, contracted, length 0.62 mm.

Fig. 2. Lateral view of genital segments of female, showing spermatophore, seminal receptacle and clear space surrounding it (cf. Fig. 4).

Fig. 3. Seminal receptacle (or part of it?).

Fig. 4. Ventral aspect of abdomen, showing one spermatophore, seminal receptacle, clear space surrounding it, deep telescoping of segments, fifth feet (cf. Fig. 2 of same female). Magnification same as for Fig. 2.

Fig. 5. Antenna of female.

Fig. 6. Spermatophores and seminal receptacle.

Fig. 7. First foot of male.

Fig. 8. Third foot of male.

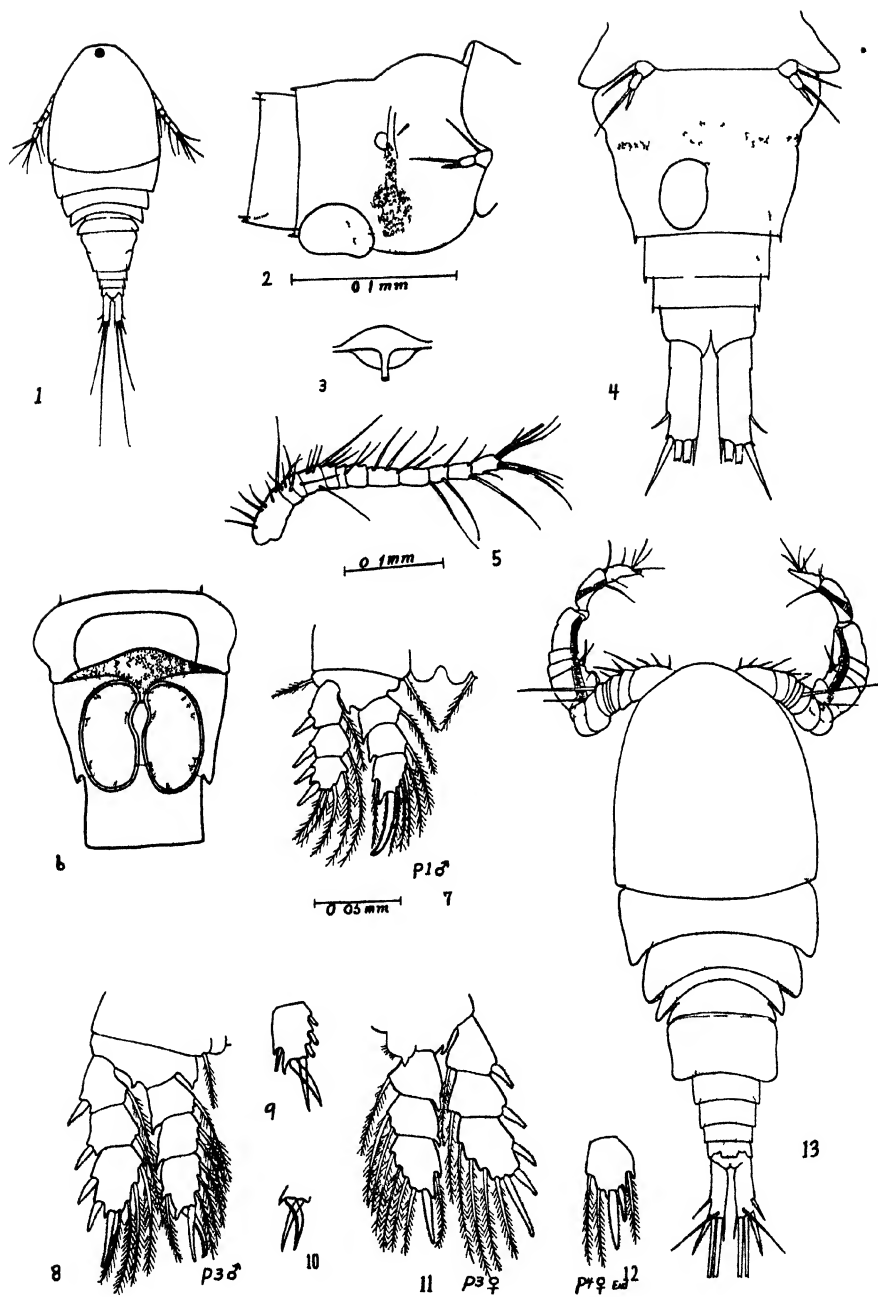
Fig. 9. Terminal segment of endopod of third foot of another male.

Fig. 10. Terminal spines of corresponding segment of a third male.

Fig. 11. Third foot of female.

Fig. 12. Terminal segment of endopodite of fourth foot of female.

Fig. 13. Dorsal aspect of male, length 0.6 mm. (more highly magnified than female).



FIGS 1-13

but the predominant plankter at certain times in the large pond at Lakeview in the pine lands of Moore County, N. C., is a species of this

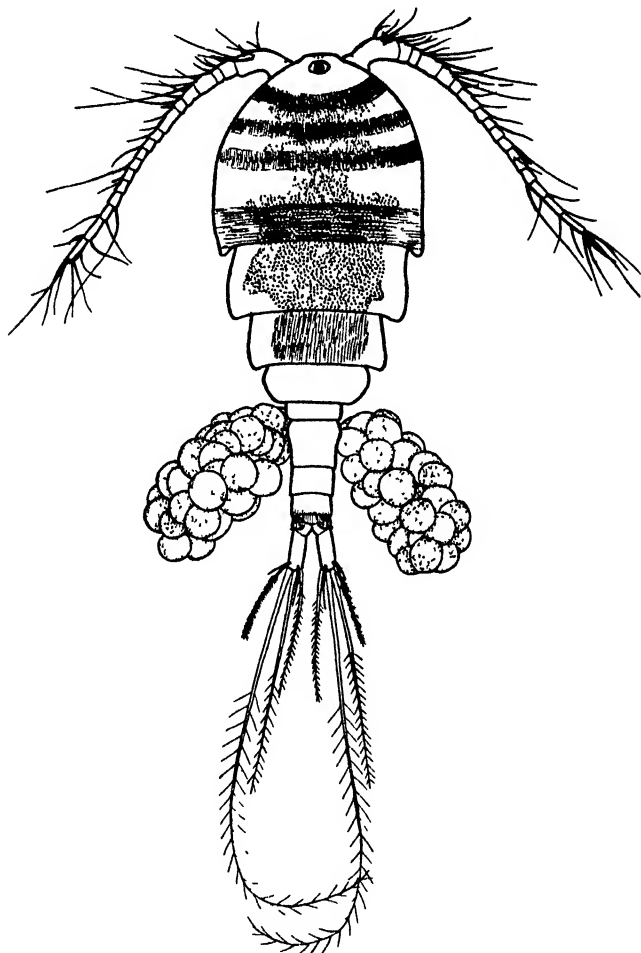


FIG. 14. *Cyclops ater*, female, from Chapel Hill, N. C. The five cross bands shaded with vertical lines were purple in life; the cross band shaded with horizontal lines was blackish purple; the stippled area represents ovary and oviducts.

restricted genus. In spring and early summer a net with 12-inch opening, drawn a couple of hundred feet through the water, would have its 100 cc. bucket more than filled with a virtually pure collection of

*Holopedium*. Very few are present in the fall. Our species seems closer to *amazonicum* than to *gibberum*.<sup>1</sup> The "lake" is really a large open pond formed forty or more years ago by the damming of a small stream. The water is distinctly but not deeply colored (translucency about 48") and somewhat acid (pH about 6); the "softness" of the water is further evidenced by the seemingly complete absence of mollusks of any kind.

Besides Cladocera of conventional form with bivalved shell and at least some foliaceous feet, there are on this continent two genera (each with one species) of the naked-bodied Cladocera (Section Gymnomera) with subcylindrical, "prehensile" feet. Hitherto these peculiar Cladocera have been reported only from northern waters. The giant, trans-

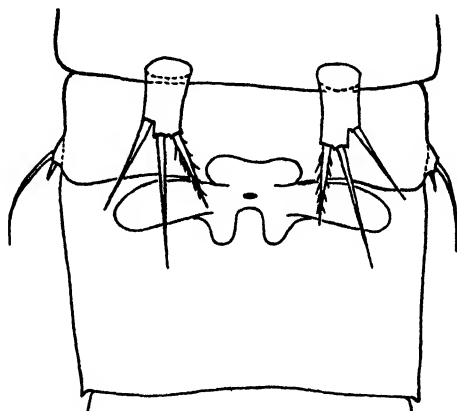


FIG. 15. *Cyclops ater*. Fifth thoracic feet and seminal receptacle

lucent, and rapacious *Leptodora* was recently collected by one of our students, Paul McKee,<sup>2</sup> in a shallow lowland lake some 40 miles from the coast. This is Phelps Lake, Washington County, N. C., embracing 16,600 acres and now a state park. Three examples only were found in a collection taken a little above the bottom where the lake was about 5 feet deep. They seem to pertain to the only known species in the Family Leptodoridae, *Leptodora kindtii* (Focke), but are very small, the largest measuring about 4.9 mm. from brow to tip of anal claws. The

<sup>1</sup> It lacks the teeth on shell and the basal spinule on the caudal spine, characteristic of *gibberum*, and is intermediate between the two known species in number of anal spines (11 or 12).

<sup>2</sup> Mr. McKee's collections were made possible through a grant from the Smith Research Fund.



species may attain a length of 18 mm. in northern lakes. Birge (1918) gives the distribution as "Limnetic in Great Lakes and small lakes in northern United States," but Kofoed (1908, p. 253) reported *L. hyalina* Lilljeborg, presumably the same species, from the expanded Illinois River near Havana, Ill. Through the courtesy of Dr. Waldo L. Schmitt of the U. S. National Museum, I have learned of the finding of *L. kindtii* in the stomachs of fish taken near Conowingo, Md., below the dam on the Susquehanna River. The collections were made by Prof. R. V. Truitt, University of Maryland, who kindly permits this record to be made, and states that *Leptodora* was found abundantly in the stomachs of *Roccus lineatus* in early summer of 1936 and 1937. Dr.

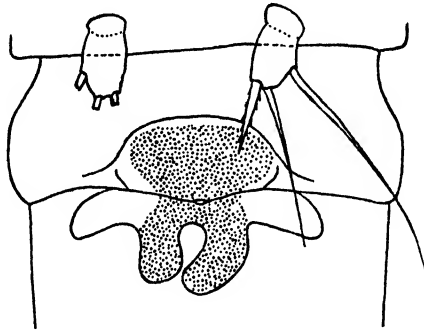


FIG. 16. Same for another individual. Genital plate not showing

Truitt's record seems to have been the southernmost for the genus prior to the present one.

Mr. McKee also obtained, February 13, 1938, from a shallow pond known as Lennon's Millpond in Robeson County near Lumberton, N. C., and some 50 miles from the ocean, a good many examples of *Polyphemus*, presumably *pediculus* (Linné), the sole species of the genus. The surface water was densely populated with algae and covered with duckweed; it contained also a good deal of Utricularia. Birge's statement regarding the distribution of the sole species in the sole American genus in the family is: "Common in Northern United States in lakes, ponds and marshes."

#### "WATER FAIRIES"

A random dip with a net in a ditch by a newly made road in a swamp just below the old Williams Mill on Cedar Creek near Society Hill, S. C., yielded a single very large and beautifully tinted phyllopod, its trans-

lucent greenish body set off by brilliant red appendages, reddish brown eyes, and a few black pigment spots. Further exhaustive search with dipnet and seine for some hundreds of yards on both sides of the road failed to yield another example. As everyone knows, male phyllopods are much rarer than females. It is noteworthy, therefore, that the single example found here was a male, of the species *Streptocephalus sealii* Ryder, and that it was, according to Dr. E. P. Creaser, the largest known example of the genus, 40 mm. in length with head bent down, or about half again as long as is normal for the species.

#### SHRIMP

Although *Palaemonetes exilipes* Stimpson, a true shrimp of fresh waters, is widely distributed and reported from about half of the states of the Union (Creaser, 1930, 1932) it seems not to have been recorded in North Carolina except in coastal counties; yet it is a regular inhabitant of the marginal waters at the bathing beach at Lakeview, 100 miles or more from the sea, and, according to a local informant, it occurs plentifully in some other waters not far distant. It is also abundant along shore in White Lake. In the fall of 1933, a dip with a net in a lagoon in a flat swampy woods along New Hope Creek, about 6 miles from Chapel Hill and a little south of the Raleigh road, yielded two examples of this shrimp; the distance from the sea coast is about 130 miles. Further intensive search on this day and succeeding days were entirely fruitless. It is impossible to say whether the two taken were merely strays from an undiscovered local habitat in the region or whether they were recent chance introductions from a distance; such chance introductions must occur or newly formed bodies of water could never become naturally stocked. For more than forty years, at least, collecting has been pursued by graduate students and others in the waters around Chapel Hill with no record of *Palaemonetes*, although the shrimp are large enough (30 mm., more or less, in length) to attract the attention of any collector; but perhaps the lagoons along the New Hope River have not often been visited.<sup>3</sup>

<sup>3</sup> Dr. Waldo L. Schmitt has kindly given me the following records of the U. S. National Museum for *Palaemonetes* from the Carolinas. Of the stations mentioned, only Orangeburg and Summerton, S. C., are remote from the coast.

Salmon Creek, N. C.

Halifax, N. C.

Edenton and Newbegun Creek,  
N. C.

Lake Mattamuskeett, Hyde  
County, N. C.

Hales Point, Halifax Co., N. C.

Summerton, S. C.

Vicinity of Wilmington, N. C.

Orangeburg, S. C.

Fresh water (cypress) pond.

It may be worth while to recall here that the largest specimen of the river shrimp, *Macrobrachium ohionis* (Smith), in the collection of the U. S. National Museum, and perhaps the largest known, was collected by Mr. J. W. Milner in 1878 at Avoca, Bertie County, N. C., at the head of Albemarle Sound, as reported by Dr. Waldo L. Schmitt (1933). Never before or since has the species been recorded from a place as far north in the Atlantic coastal plain.

ANNOTATED LIST OF CYCLOPOID COPEPODS OF THE REGION OF CHAPEL HILL, N. C.

To complete the record of copepods now known in the region of Chapel Hill, a list of the cyclopoids follows. (The locality is Chapel Hill unless otherwise stated.)

1. *Cyclops (Macrocyclops) ater* Herrick. This large species is always rare, but at Chapel Hill it has been found at several places along Bolin's Creek in quiet water; we record it also from Lakeview and Sweetheart Lake, both near Southern Pines, from White Lake, Bladen County, and from Greenfield Pond near Wilmington. (I have found it also in Quaker Lake in Allegany State Park, N. Y.)
2. *Cyclops (Macrocyclops) albidus* Jurine. Common in pools.
3. *Cyclops (Macrocyclops) fuscus* Jurine. Common in pools.
4. *Cyclops (Eucyclops) serrulatus* Fischer. Common in small waters.

A *serrulatus*-like form with extremely long furca ( $\frac{FW}{FL} = 0.14$ )

has been found in a pond in Strowd's Low Ground at Chapel Hill, but only further study, impracticable as yet, would place it as a variant of *serrulatus* or as another species. A form with very short furca ( $\frac{FW}{FL} = 0.45$ ) occurs in bottom fauna of White Lake.

The group clearly requires further study.

5. *Cyclops (Eucyclops) prasinus* Fischer. Common in lakes, including University Lake; found also in a small pond across Bolin's Creek.
6. *Cyclops (Paracyclops) fimbriatus* Fischer. Not infrequent in marshes.
7. *Cyclops (Ectocyclops) phaleratus* Koch. Glen Burnie Marsh.
8. *Cyclops (Cyclops) gigas* Claus (?). A species closely related to *viridis*, taken from the bayou previously mentioned, but now non-existent, was thought by Marsh to be probably *C. magnus*,

described by him from Canada. Kiefer (1929) regards *magnus* as synonymous with the more widely distributed *C. gigas* Claus. Until this group of *viridis* in America has been more thoroughly studied by someone familiar with the European *viridis* we think that all records of the group, including our own, are questionable (see my paper 1934a, p. 271).

9. *Cyclops (Cyclops) vernalis* Fischer. Very common in several forms commonly called *americanus (robustus)*, *parvus*, *brevispinosus*.
10. *Cyclops (Cyclops) bicuspidatus* Claus. Durham City Reservoir.
11. *Cyclops (Cyclops) venustoides* Coker. In some meadows and spring runs.
12. *Cyclops (Cyclops) exilis* Coker. In spring runs.
13. *Cyclops (Cyclops) crassicaudis* Sars. See comment above, p. 77.
14. *Cyclops (Cyclops) nanus* Sars. White Lake (Coker, 1938?).
15. *Cyclops (Cyclops) varicans* Sars. Strowd's Low Ground.
16. *Cyclops (Cyclops) bicolor* Sars. Greenfield Pond, near Wilmington.
17. *Cyclops (Orthocyclops) modestus* Herrick. Under ice in Bolin's Creek, and at Sparrow's Mill.
18. *Cyclops (Mesocyclops) leuckarti* Claus. Common in lakes including University Lake.

#### SUMMARY

1. The calanoid copepods (5 species) collected by the writer in North Carolina, with one exception, were far out of the previously accepted ranges of distribution for the several species.

2. American harpacticoid copepods are too little known for the formulation of distribution records of significance, but two of the nine known species of the region are of a type previously supposed to be distinctly northern, if not a glacial relict, and a third, not now distinguishable from a European species, had been found in this country only in waters of western New York tributary to the Mississippi (see author's paper of 1938). The last mentioned and one of the first two are from White Lake.

3. Records of *Cyclops crassicaudis* in America are extremely rare. Its occurrence at Chapel Hill is very peculiar, but perhaps suggestive as to the kinds of waters in which search for this species should be made everywhere.

4. *Holopedium*, *Leptodora*, and *Polyphemus* are recorded from shallow waters of the coastal plain.

5. The largest *Streptocephalus* of record at the time (and perhaps

still) was collected as a unique specimen (a male) in a newly formed ditch in South Carolina.

6. The range of *Palaemonetes exilipes* Stimpson is extended by records at Lakeview and a unique record at Chapel Hill.

7. Fifteen species of the old broad genus *Cyclops* are definitely identified from the region of Chapel Hill, N. C., besides one from Wilmington, one from White Lake, and one or two others that are not now positively identifiable.

8. The appearance of anomaly in a good many of the records cited probably arises in part from the inadequacy of knowledge of the crustacean fauna of the southeastern United States. The need and the opportunity for studies of fresh-water Crustaceans of the region are clearly indicated.

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# PLANKTON ROTATORIA FROM NORTH CAROLINA

By ELBERT H. AHLSTROM

## PLATES 6-9

This paper is based upon a rather large group of plankton samples collected in pools, ponds, streams, and lakes in many parts of the state of North Carolina. The three large geographic divisions of the state, the coastal plain, the central piedmont plateau, and the western mountainous region, are all adequately represented. The greatest diversity of forms was found in the material from the coastal region. Material from over a hundred different habitats was examined.

All determinations were made from preserved material, killed by adding Transeau's solution (6 parts water, 3 parts alcohol, 1 part formaldehyde) to collections made with a # 20 bolting silk plankton net. Loricata rotifers are readily identifiable in preserved material; in fact, it is necessary to have most loricata rotifers in a contracted condition to see the distinguishing characters used in their classification. Soft-bodied rotifers are identified with difficulty in preserved material. Their distinguishing features are best seen in expanded living material, and they should be narcotized before killing if their distinguishing characters are to be retained in preserved material. The soft-bodied forms in the North Carolina samples, belonging principally to the notommatid and bdelloid groups, are not adequately treated in this paper. However, such soft-bodied forms were usually few in numbers in the North Carolina samples, being outnumbered several hundred to one by loricata forms in most samples.

Plankton rotatoria in shallow bodies of water are composed largely of adventitious species. There are few truly limnetic species of rotifers. In the discussion that follows no attempt is made to segregate euplanktons from facultative planktons or from forms accidentally occurring in the plankton whose usual habitat is the littoral. Any organism taken in plankton samples is considered in this paper as being a plankton organism.

This is the first extensive faunal list of North Carolina rotifers. Rotifers have been intensively studied in the eastern United States

from the following localities: Mt. Desert Island region of Maine (Myers 1931-4), from the Adirondack region of New York (Myers 1937), from Atlantic County in New Jersey (references scattered through many papers of Myers and Harring and Myers), from Washington, D. C. (Harring 1914), and from Florida (Ahlstrom 1934).

The rotatoria found in bodies of water with a pH below 7.0 are quite different from those taken in alkaline habitats. There is a typical alkaline water fauna, having exclusively such genera as *Brachionus*, *Platylas* and *Notholca*; there are many species of other genera that belong definitely to the alkaline fauna alone. Similarly, there is a large number of species whose distribution is limited to acid water associations. Such species are a reliable index to the hardness or softness of a certain body of water. There is a third group of species, tolerant of a rather wide range of pH, which are found in both acid and alkaline habitats. As a rule, loricate rotifers are much more abundant in alkaline fresh waters than in soft water habitats; the number of individuals per unit volume is often many times greater in alkaline habitats than in acid. Acid water habitats, on the other hand, have a much greater diversity of species than hard water associations, and notammatid rotifers are much more common than in hard waters. In North Carolina the bodies of water on the coastal plain are mostly neutral or acid, while the ponds and streams in the piedmont and mountainous regions are commonly hard water associations.

I am deeply indebted to Larry Whitford of the Department of Botany of North Carolina State College, who collected all the samples upon which this paper is based. Mr. Whitford is making an algal survey of the state, in the course of which he has gathered a great number of collections of plankton organisms. He kindly divided many of these samples so that the author could study the rotatorian fauna. I also deeply appreciate the aid given by Frank J. Myers of Ventnor, N. J., during the course of this investigation.

#### SPECIES OF NORTH CAROLINA PLANKTON ROTATORIA

The number of bdelloid and notommatid rotifers listed is few. The contracted condition of these organisms made their specific determination difficult or impossible. The loricate genera of *Lepadella*, *Colurella*, and *Testudinella* were very widely distributed, and represented by a rather large number of species. Neither *Colurella* nor *Testudinella* is a large genus, so the number of species recorded for the state is noteworthy. Although the list of species for *Lecane* and *Monostyla* are



rather large, yet the number of species of these sizable genera recorded for the state is disappointing; neither genus presents near the diversity of species in North Carolina that it does in Florida or New Jersey. *Brachionus* is not well represented in North Carolina. *Brachionus angularis* and *Brachionus havanaensis* are rather widely distributed, but many common species are rare or absent. *Brachionus calyciflorus* and *Brachionus caudatus* were not recorded at all for the state, though both are very common and widely distributed in alkaline habitats elsewhere in the United States. On the other hand, the alkaline water species, *Platytias patulus*, is widely distributed over North Carolina. Among the Trichocercids, the subgenus *Diurella* was well represented in numbers and species in the state, *Trichocerca rousseleti*, in particular, was very widely distributed and often common in the samples; in the subgenus *Rattulus*, *Trichocerca multicrinis* was often abundant and several other species were common, yet noteworthy by their rarity or absence was the *bicristata-mucosa-cristata-rattus* group of species (a group which is widely distributed in Ohio and elsewhere).

The symbols after specific names have the following significance: A, widely distributed (often common); C, seen in more than ten samples; F, seen in five to ten samples; R, seen in two to four samples; S, seen in but a single collection.

*Anuraeopsis fissa* (Gosse), A.  
*Anuraeopsis fissa* var. *navicula* (Rousselet), R.  
*Ascomorpha saltans* Bartsch, R.  
*Asplanchna brightwellii* Gosse, R.  
*Asplanchna priodonta* Gosse, F.  
*Brachionus angularis* Gosse, A.  
*Brachionus budapestinensis* Daday, R.  
*Brachionus havanaensis* Rousselet, C.  
*Brachionus plicatilis* Müller, R.  
*Brachionus quadridentatus* Hermann, F.  
*Brachionus urceolaris* Muller, R.  
*Brachionus zahniseri* Ahlstrom, R.  
*Cephalodella auriculata* (Müller), R.  
*Cephalodella forficula* (Ehrenberg), R.  
*Cephalodella gibba* (Ehrenberg), F.  
*Cephalodella panarista* Myers, R.  
*Cephalodella sterea* (Gosse), S.  
*Chromogaster ovalis* (Bergendal), A.  
*Colurella adriatica* Ehrenberg, S.  
*Colurella bicuspidata* (Ehrenberg), A.  
*Colurella colurus* (Ehrenberg), S.

*Colurella hindenbergi* Steinecke, S.  
*Colurella mucronulata* sp. nov., S.  
*Colurella obtusa* (Gosse), C.  
*Colurella sulcata* (Stenroos), R.  
*Colurella tessellata* (Glasscott), R.  
*Conochiloides coenobasis* Skorikov, R.  
*Conochiloides dossuarius* (Hudson), R.  
*Conochiloides exiguus* sp. nov., S.  
*Conochiloides natans* (Seligo), S.  
*Conochilus unicornis* Rousselet, A.  
*Dapidia calpidia* Myers, S.  
*Dicranophorus prionacis* Harring and Myers, S.  
*Dissotrocha aculeata* (Ehrenberg), F.  
*Dissotrocha macrostyla* (Ehrenberg), A.  
*Dipleuchlanis propatula* (Gosse), R.  
*Eosphora anthadis* Harring and Myers, R.  
*Euchlanis dilatata* Ehrenberg, C.  
*Euchlanis meneta* Myers, F.  
*Euchlanis parva* Rousselet, S.  
*Euchlanis pellucida* Harring, S.

- Euchlanis phryne* Myers, R.  
*Euchlanis triquetra* Hudson and Gosse, R.  
*Filina longiseta* (Ehrenberg), F  
(usually abundant when present)  
*Filina longiseta* var. *terminalis* (Plate), R.  
*Gastropus hytopus* (Ehrenberg), C.  
*Gastropus styliifer* Imhof, A.  
*Kellicottia bostoniensis* (Rousselet), A.  
*Keratella cochlearis* (Gosse), A (most common species in state)  
*Keratella curvicornis* (Ehrenberg), F.  
*Keratella paludosa* (Lucks), C.  
*Keratella serrulata* (Ehrenberg), R.  
*Lecane arcua* Harring, F.  
*Lecane aspasia* Myers, R.  
*Lecane climacois* Harring and Myers, F.  
*Lecane crepida* Harring, R.  
*Lecane curvicornis* (Murray), F.  
*Lecane doryssa* Harring, S.  
*Lecane flexilis* (Gosse), C.  
*Lecane grandis* (Murray), S (Brackish Creek, Bayboro)  
*Lecane hastata* (Murray), S.  
*Lecane hornemanni* (Ehrenberg), R.  
*Lecane leontina* (Turner), F.  
*Lecane ludwigii* (Eckstein), R.  
*Lecane luna* (Müller), A.  
*Lecane luna* var. *presumpta* var. nov., R.  
*Lecane methoria* Harring and Myers, S.  
*Lecane mira* (Murray), S.  
*Lecane nana* (Murray), R.  
*Lecane ohioensis* (Herrick), R.  
*Lecane pertica* Harring and Myers, R.  
*Lecane plesia* Myers, S. (Brackish Creek, Bayboro)  
*Lecane satyrus* Harring and Myers, R.  
*Lecane signifera* (Jennings), A.  
*Lecane stichaea* Harring, F. (common Lake Mattamuskeet)  
*Lecane stokesii* (Pell), R.  
*Lecane tenuiseta* Harring, F.  
*Lecane ungulata* (Gosse), C.  
*Lepadella acuminata* (Ehrenberg), A.  
*Lepadella akrobelles* Myers, R.  
*Lepadella apsicora* Myers, R.  
*Lepadella apsidea* Harring, R.  
*Lepadella benjamini* Harring, F.  
*Lepadella cristata* (Rousselet), R.  
*Lepadella cyrtopus* Harring, S.  
*Lepadella dactyliseta* (Stenroos), F.  
*Lepadella latusinus* var. *americana* Myers, S.  
*Lepadella ovalis* (Müller), S.  
*Lepadella patella* (Müller), A.  
*Lepadella quadricarinata* (Stenroos), R.  
*Lepadella quinquecostata* (Lucks), F.  
*Lepadella rhomboides* (Gosse), C.  
*Lepadella salisburyi* Ahlstrom, S (Lake Waccamaw)  
*Lepadella triptera* Ehrenberg, R.  
*Lepadella venefica* Myers, F.  
*Lepadella whitfordi* sp. nov., R.  
*Lophocharis salpina* Ehrenberg, F.  
*Macrochaetus collinsii* (Gosse), R.  
*Macrochaetus longipes* Myers, S. (Cathernis Lake)  
*Macrochaetus subquadratus* Perty, R.  
*Monommata grandis* Tessin, F.  
*Monommata longiseta* (Müller), F.  
*Monommata maculata* Harring and Myers, R.  
*Monostyla bifurca* Bryce, R.  
*Monostyla bulla* Gosse, A.  
*Monostyla closteroerca* Schmarda, A.  
*Monostyla cornuta* (Müller), C.  
*Monostyla crenata* Harring, A.  
*Monostyla elachis* Harring and Myers, R.  
*Monostyla furcata* Murray, C.  
*Monostyla hamata* Stokes, A.  
*Monostyla harringi* Ahlstrom, S (Brackish Creek, Bayboro)  
*Monostyla lunaris* (Ehrenberg), A.  
*Monostyla monostyla* (Daday), S.  
*Monostyla obtusa* (Murray), R.  
*Monostyla ornata* Harring and Myers, S.  
*Monostyla perplexa* sp. nov., S.  
*Monostyla quadridentata* Ehrenberg, A.  
*Monostyla stenroosi* Meissner, R.  
*Monostyla telhis* Harring and Myers, S.  
*Monostyla unguitata* Fadeev, S.  
*Monostyla whitfordi* sp. nov., S.

- Mytilina trigona* (Gosse), S (Pond, Morehead City)  
*Mytilina ventralis* (Ehrenberg), R.  
*Notholca striata* (Müller), S.  
*Notholca striata acuminata* (Ehrenberg), S.  
*Notommata copeus* Ehrenberg, F.  
*Notommata pachyura* (Gosse), S.  
*Pedalia mira* (Hudson), C.  
*Platygaster patulus* (Müller), A.  
*Platygaster quadricornis* (Ehrenberg), R.  
*Pleurotrocha robusta* (Glasscott), R.  
*Ploesoma formosum* Myers, S. (White Lake)  
*Ploesoma lenticulare* Herrick, F.  
*Ploesoma truncata* (Levander), C.  
*Polyarthra euryptera* Wierzejski, A.  
*Polyarthra trigla* Ehrenberg, A.  
*Pompholyx complanata* Gosse, R.  
*Proales doliaris* (Roussetlet), R.  
*Reticula melandocus* (Gosse), R.  
*Rotaria neptunia* (Ehrenberg), R.  
*Scaridium longicaudum* (Müller), R.  
*Squatinella mulica* (Ehrenberg), R.  
*Synchaeta longipes* Gosse, F.  
*Synchaeta pectinata* Ehrenberg, A.  
*Synchaeta stylata* Wierzejski, A.  
*Synchaeta tremula* Ehrenberg, S.  
*Taphrocampa annulosa* Gosse, S.  
*Taphrocampa selenura* Gosse, R.  
*Testudinella angulata* Myers, R.  
*Testudinella caeca* (Parsons), R.  
*Testudinella dentata* Myers, S.  
*Testudinella dicella* Myers, R.  
*Testudinella discoidea* sp. nov., R.  
*Testudinella incisa* (Ternetz), C.  
*Testudinella parva* (Ternetz), F.  
*Testudinella parva* var. *bidentata* (Ternetz), R.  
*Testudinella patina* (Hermann), F.  
*Testudinella reflexa* (Gosse), C.  
*Trichocerca (Diurella) bidens* (Lucks), S.  
*Trichocerca (Diurella) brachyura* (Gosse), F.  
*Trichocerca (Diurella) collaris* (Roussetlet), S.  
*Trichocerca capucina* (Wierzejski), F.  
*Trichocerca cylindrica* (Imhof), C.  
*Trichocerca (Diurella) edmondsoni* (Myers), S.  
*Trichocerca elongata* (Gosse), S.  
*Trichocerca (Diurella) insignis* (Herrick), F.  
*Trichocerca lata* (Jennings), S (White Lake)  
*Trichocerca longiseta* (Schränk), F.  
*Trichocerca mucosa* (Stokes), R.  
*Trichocerca mucripes* sp. nov., S.  
*Trichocerca multicrinis* (Kellicott), A.  
*Trichocerca (Diurella) porcellus* (Gosse), F.  
*Trichocerca pusillus* (Jennings), A.  
*Trichocerca rosea* (Stenroos), R.  
*Trichocerca (Diurella) rotundata* Myers, F.  
*Trichocerca (Diurella) roussetleti* (Voigt), A.  
*Trichocerca scipio* (Gosse), F.  
*Trichocerca (Diurella) similis* (Wierzejski) = *Diurella stylata* Eyferth, A.  
*Trichocerca stylata* (Gosse), S.  
*Trichocerca (Diurella) sulcata* (Jennings), S.  
*Trichocerca (Diurella) tenuior* (Gosse), C.  
*Trichocerca (Diurella) tigris* (Müller), F.  
*Trichocerca (Diurella) tortuosa* (Myers), S.  
*Trichocerca (Diurella) weberi* (Jennings), F.  
*Trichotria spinifera* (Western), R.  
*Trichotria tetractis* (Ehrenberg), C.  
*Trichotria tetractis* var. *caudata* (Lucks), R.  
*Tripleuchlanis plicata* (Levander), S (Brackish Creek, Bayboro)

## NEW AND UNUSUAL ROTIFERS

**Anuraeopsis fissa** var. **navicula** (Rousselet)

*Anuraeopsis navicula* Rousselet, Zool. Jahrb. Syst. **29**: 669, 1910.

*Anuraeopsis navicula* var. *coelata* de Beauchamp, Linnean Soc. Jour. Zool. **38**: 238, fig. 3, 1932.

The chief distinction between var. *navicula* and *A. fissa vera* is in the pattern of ridges and the tuberculate ornamentation on the lorica of the variety (*A. fissa vera* is but lightly stippled). Supposed differences in the size and shape of the lorica between the two forms breaks down when a series of forms of the two are studied. Even the prominence of ornamentation is a very variable feature in this species, and has been shown to have little or no taxonomic value in the related genus *Brachionus*. I first encountered the variety in material from Parahyba, Brazil, and have since observed it in material from Florida and North Carolina.

**Brachionus zahniseri** Ahlstrom

Ahlstrom, Trans. Am. Micro. Soc. **53**: 256, pl. 25, fig. 1, 2, 1934.

Observed in several habitats in North Carolina, being very common in freshwater material from Bayboro. It was rare in a sample from a brackish creek at Bayboro in which *Brachionus plicatilis*, a characteristic brackish species, was common. It must therefore be tolerant of highly alkaline situations. Some specimens from North Carolina had the lorica distinctly pustulate.

**Colurella hindenburgi** Steinecke. Pl. 6, figs. 3, 4.

Steinecke, Schrift. Phys.-ökonom. Ges. Königsberg i P., Jahrg. **57**: 90, 97, fig. 4, 1916; Hauer, Verhandl. Naturwiss. Vereins in Karlsruhe **31**: 72, figs. 11a-b, 1935.

This small *Colurella* is closely allied to *Colurella obtusa*. The body is more compressed and the toes are much longer. The toes narrow rapidly, end in long, bristle-like tips, and are rather undulate.

The lorica measures  $63\mu$  long,  $39\mu$  deep, and  $27\mu$  broad. The toes are  $27\mu$  long.

*Colurella hindenburgi* was rare in a freshwater pond at Currituck Sound (May 23, 1937).

**Colurella mucronulata** sp. nov. Pl. 6, figs. 1, 2.

The lorica is fusiform and greatly compressed from the dorsal view; it is irregularly oval in lateral view, rounded posteriorly, and pointed anteriorly. The lorica is ornamented with a number of longitudinal ridges extending the length of the lorica. The first and second foot joints are relatively short and subsquare, the terminal joint is somewhat longer. The toes are very long; they narrow rapidly to extremely slender, drawn-out tips.

Total length  $168\mu$ ; length of lorica  $109\mu$ , width  $38\mu$ , depth  $48\mu$ ; length of terminal foot joint  $12\mu$ ; of toes  $40\mu$ .

*Colurella mucronulata* was rare in a mill pond near Pineola (June 18, 1936). It is larger than any described species of *Colurella*, and is the only species pointed anteriorly. In side view it greatly resembles a *Lepadella* in the same position. However, in dorsal view it is seen to be a typical *Colurella*. Its pattern of ornamentation resembles *Colurella sulcata*.

**Colurella sulcata** (Stenroos). Pl. 6, fig. 5.

*Metopidia sulcata* Stenroos, Acta Soc. Fauna Flora Fennica 17: 166, pl. 2, figs. 27-29, 1898.

*Colurella sulcata* Haring, Bull. U. S. Nat. Mus. 81: 30, 1913; Fadeev, Proc. Nat. Soc. Kharkov. 50(1): 9, fig. 9, 1925.

This rugose *Colurella* is apparently widely distributed in the United States in small numbers. It was observed from several localities in North Carolina. The material I have seen of this species differs from the figure of Stenroos in the length of the terminal foot joint: Stenroos' figure shows this to be little longer than the other joints, but in North Carolina material it is twice as long. Fadeev figures this species with a long terminal foot joint.

Length of lorica  $78\mu$ , depth  $31\mu$ , length of last foot joint  $15\mu$ , toes  $24\mu$ .

**Conochiloides coenobasis** Skorikov. Pl. 7, figs. 7, 9.

Skorikov, Arbeiten ichtyolog. lab. Kaspi-Wolg. Fisch.-Ver. Astrachan 3(5): 30, figs. 1, 2, 1914.

This species is characterized by the ventral antennae arising from a mound-like basal portion nearly as long as the antennae. The stalk-like foot is not particularly long, and on preserved specimens is mostly retracted into the body.

The mastax is of the malleo-ramate type. The right ramus is slightly larger than the left. There are three slender, opposing teeth,

clubbed at their tips, as well as a number of thin, closely crowded accessory teeth in each uncus. Length of trophi  $34\mu$ .

This species is closely allied to *Conochiloides natans*. In the latter species the unci formula is  $\frac{5+}{5+}$  (length of trophi  $42\mu$ ) in contrast to  $\frac{3+}{3+}$  for *Conochiloides coenobasis*. *Conochiloides natans* is also somewhat larger in size, and has the ventral antennae free for their entire length and not situated on a mound-like basal portion.

*Conochiloides coenobasis* was observed in Murfreesboro mill pond. I identify the North Carolina specimens with Skorikov's species on the basis of the ventral antennae; Skorikov does not figure or discuss the mastax.

*Conochiloides exiguus* sp. nov. Pl. 7, figs. 8, 11.

Size small, body pyriform with a long, stalk-like foot, longer than the body length on expanded specimens. Ventral antennae joined for nearly their entire length. The mastax is of the malleo-ramate type. Rami are asymmetric, the right ramus is slightly larger than the left. There are four slender teeth clubbed at their tips in the right incus, as well as a number of closely crowded accessory teeth; the left incus has the last tooth bifurcate, and possesses three other clubbed teeth as well as a number of accessory teeth. Length of trophi  $20\mu$ .

Total length of body and stalk-like foot  $170-190\mu$ .

*Conochiloides exiguus* was common in Murfreesboro mill pond. It is closely related to *Conochiloides dossuarius*. It is much smaller than the latter species, however, and has the unci formula of  $\frac{1^{+1}+3^{+}}{4^{+}}$  in contrast to the unci formula for *Conochiloides dossuarius* of  $\frac{1^{+1}+2^{+}}{5^{+}}$ . The ventral antennae of *Conochiloides exiguus* are joined for even more of their length than are those of *Conochiloides dossuarius*. All individuals noted were solitary. No gelatinous tube was apparent in the preserved material.

*Kellicottia*, genus novum

Brachionid rotifers with unpaired occipital spines of unequal lengths, one spine being as long as the body proper. Lorica elongated conical, terminating in a long, thin posterior spine. Lorica somewhat compressed dorso-ventrally. Mental margin unornamented, with a shallow median sinus. Body smooth or lightly stippled.

Type species: *Kellicottia longispina* (Kellicott) = *Anuraea longispina* Kellicott = *Notholca longispina* (Kellicott).

***Kellicottia longispina* (Kellicott)**

*Anuraea longispina* Kellicott, Am. Jour. Micro. Pop. Sci. 4: 19, fig., 1879.

*Anuraea spinosa* Imhof, Zool. Anz. 6: 470, fig. 2, 1883.

*Notholca longispina* Hudson and Gosse, Rotifera, 2: 125, pl. 28, fig. 6, 1886.

Occipital spines six: lateral spines subequal and quite long, the left lateral spine somewhat longer than the right; intermediate spines quite short and needle-like; left median spine only slightly longer than intermediate spines, right median spine very long, being nearly half the total length of organism; spines are all very thin and taper to needle-like tips, margin slightly serrate. Mental margin elevated, truncate, with a rather deep U-shaped central sinus. Body proper elongate-conical, though somewhat compressed dorso-ventrally, tapers to a very long and thin posterior spine (slightly shorter than right median occipital spine). Body unornamented save for strengthening ridges arising from base of median spines.

Total length (specimens from Lake Washington near Seattle, Washington)  $625\mu$ ; length of occipital spines reading from left to right  $144-29-42-280-28-118\mu$ ; length of posterior spine  $224\mu$ , width of body  $56\mu$ .

*Notholca longispina* has not been observed in material from North Carolina, although it undoubtedly occurs. It is a truly limnetic species, found in temperate lakes in all parts of the world. It was originally described from Lake Erie.

***Kellicottia bostoniensis* (Rousselet). Pl. 9, fig. 1.**

*Notholca bostoniensis* Rousselet, Jour. Quekett Micro. Club, ser. 2, 10: 337, pl. 21, figs. 1-3, pl. 27, fig. 4, 1908.

Occipital spines four: lateral spines short, recurved near their tips, needle-like; left median spine much longer than right, anterior spines somewhat serrate. Mental margin with a V-shaped central notch dividing the margin into two rounded lobes. Greatest width of body near the center, from which the lorica tapers rapidly to a rather long and thin posterior spine. Body in side view seen to arch dorsally, and both the posterior spine and the long anterior spine are curved ventrally. Short strengthening ridges arise from bases of median

occipital spines. Lorica is ornamented on some individuals with a pattern of longitudinal striations made up of closely placed tubercles; other specimens appear quite smooth.

Total length  $364\mu$ ; length of anterior spines reading from left to right  $26-144-44-24\mu$ ; length of posterior spine  $118\mu$ ; width of body  $52\mu$ .

Originally described from Boston, this species seems to be widely distributed in eastern United States, being reported from Florida to New Brunswick (I have seen it in material from Lake Superior). It is widely distributed in North Carolina.

*Kellicottia bostoniensis* differs from *Kellicottia longispina* in its consistently smaller size; in having four anterior spines rather than six, and in different proportions between the spines; and in the shape of the body.

The genus *Kellicottia* is distinguishable from all other brachionid genera by the character of the occipital spines, which are not paired as is the case in all other genera possessing anterior spines, but are of unequal lengths. All species included in the genus *Notholca* have three pairs of spines, and are bilaterally symmetrical, so that a line drawn through the median bisects the occipital margin into corresponding sets of spines (*Notholca japonica* (Marukawa) = *Pseudonotholca japonica* Marukawa 1928, = *Notholca quadraspinata* Myers 1936 has but two pairs of occipital spines). The occipital margin of *Kellicottia* is never bilaterally symmetrical. No other genus of brachionids has occipital spines of such length as in *Kellicottia*.

The family Brachionidae will include the following genera (some investigators include a number of other genera in this family):

Family Brachionidae

Subfamily Brachioninae

Genus *Brachionus* (including *Schizocerca*)

Genus *Platylas*

Subfamily Anuraeinae

Genus *Keratella* (= *Anuraea*)

Genus *Notholca* (including *Pseudonotholca*)

Genus *Kellicottia*

Genus *Anuraeopsis*

***Lecane luna* var. *presumpta* nov. var. Pl. 7, fig. 1.**

The outline of the lorica is very broadly ovate, its greatest width being about four-fifths of the length. The anterior dorsal margin is nearly straight or very slightly convex. The ventral margin has a conspicuous, U-shaped central notch, rounding upwards at the sides.



The dorsal plate is broadly ovate, and somewhat truncate posteriorly; the ventral plate is oval, slightly narrower than the dorsal; it has a transverse fold in front of the foot. The posterior segment is small and rounded; it projects slightly beyond the dorsal plate. The first foot joint is distinct and widest posteriorly, the second truncate pyriform. The toes are about a third of the total length, are parallel-sided, and end in a distinct claw with a small basal spicule.

Total length  $165\mu$ ; length of dorsal plate  $121\mu$ , of ventral plate  $128\mu$ ; width of dorsal plate  $108\mu$ , of ventral plate  $103\mu$ , of anterior ventral margin  $66\mu$ ; length of toe without claw  $41\mu$ ; claw  $11\mu$ .

*Lecane luna* var. *presumpta* is rather widely distributed; I have seen it in collections from a number of localities in the United States. I am calling attention to this variation by making it a variety. It has characters definitely intermediate between those of *Lecane luna* and *Lecane papuana*. The nearly straight anterior dorsal margin is similar to *Lecane papuana*, as is the anterior sinus in the ventral plate. *Lecane papuana* differs in having two projecting lobes on either side of the central, anterior ventral sinus. *Lecane papuana* is subtropicopolitan in distribution, and has not been found in the United States other than Florida. The record of *Lecane papuana* for Wisconsin by Harring and Myers (1922) is erroneous, and probably refers to the variety. The new variety is proportionately narrower than *Lecane luna*, has the dorsal plate nearly truncate posteriorly, and differs greatly from *Lecane luna* in the character of the anterior margins.

**Lepadella akroboles** Myers. Pl. 6, figs. 10, 12.

Myers, Am. Mus. Novitates No. 760, p. 5, figs. 13-15, 1934.

The North Carolina material agrees very closely with Myers' description, except as regards the cross sectional view of the body. There is observable in sectional view not a single rounded dorsal elevation, but three distinct ridges. Observed in material from Lake Mattamuskeet and from a gravel pit pool at Swannanoa.

**Lepadella dactyliseta** (Stenroos). Pl. 6, fig. 6.

*Metopidia dactyliseta* Stenroos, Acta Soc. Fauna Flora Fennica 17 (1): 165, pl. 3, fig. 1, 1898.

*Lepadella dactyliseta* Harring, Proc. U. S. Nat. Mus. 51: 547, pl. 92, figs. 1-3, 1916; Hauer, Verhandl. Naturwiss. Vereins in Karlsruhe 31: 88, fig. 19, 1935.

*Metopidia rottenburgi* Lucks, Rotatorienfauna Westpreussens, p. 127, fig. 48, 1912.

Total length  $112\mu$ ; length of lorica  $86\mu$ , width of lorica  $66\mu$ , depth of ventral head opening  $18\mu$ ; width at posterior end of foot opening  $22\mu$ ; length of toes  $35\mu$ .

*Lepadella dactyliseta* is rather widely distributed in North Carolina. The only other American record is from Norfolk, Va. It has apparently been overlooked by other American investigators.

***Lepadella quadricarinata* (Stenroos). Pl. 6, fig. 13.**

*Metopidia quadricarinata* Stenroos, Acta Soc. Fauna Flora Fennica 17(1): 165, pl. 3, fig. 2, 1898; Lucks, Rotatorienfauna Westpreussens, p. 121, fig. 41, 1912.

*Lepadella quadricarinata* Harring, Bull. U. S. Nat. Mus. 81: 64, 1913; Hauer, Beiträge Naturkund. Forsch. Sudwestdeutschland 1(1): 143, pl. 1, figs. 6a-c, 1936.

Harring (1916) in his review of the genus *Lepadella* considered this as a synonym of *Lepadella patella*. Hauer (1936) considers it distinct. I have noted this species as very common in a collection containing *Lepadella patella* as well, and the two are always sharply separable. *Lepadella quadricarinata* is proportionately wider, and has more prominent and more acute points at the ventral margins of the head opening. The four short dorsal ridges are always developed. The dorsal plate is always somewhat prolonged over the foot opening, and is truncate. The comparative measurements of *Lepadella quadricarinata* and *Lepadella patella* from the same habitat follows:

	<i>L. quadricarinata</i>	<i>L. patella</i>
Total length.....	$126\mu$	$105\mu$
Length lorica .....	$100\mu$	$86\mu$
Width lorica .....	$80\mu$	$61\mu$
Width at anterior end.....	$26\mu$	$18\mu$
Depth foot groove.....	$26\mu$	$24\mu$
Length terminal foot joint.....	$9\mu$	$7.5\mu$
Length toes .....	$25\mu$	$22\mu$

Apparently this species is rather widely distributed.

***Lepadella rhomboides* (Gosse). Pl. 6, fig. 9.**

This widely distributed Lepadellid had a variant in Lake Mattamuskeet in which the toes are much longer than is usual.

Total length  $141\mu$ , length of lorica  $95\mu$ ; width  $62\mu$ , width anterior margin  $28\mu$ ; length of last foot joint  $17\mu$ , of toes 35 (-39) $\mu$ .

***Lepadella whitfordi* sp. nov. Pl. 6, figs. 7, 8, 11.**

The body is ovoid in outline; the greatest width is slightly anteriorward of the middle of the body; the body terminates posteriorly in a bluntly pointed projection. Four low projections arise near the anterior margin of the dorsum, expand slightly toward the center of the dorsal plate and gradually diminish in width posteriorward; in lateral view the dorsal projections appear as four ridges. The dorsal sinus is moderately deep and broadly U-shaped, the ventral sinus is deeper and broadly V-shaped; the collar is lightly stippled.

The foot groove is narrow, and slightly flaring posteriorly. The foot is relatively short; the terminal joint is longer than the first and second joints, but not so long as their combined length. The toes are very long; they diminish abruptly to extremely slender, drawn-out tips.

Length of lorica  $106\mu$ ; foot groove  $28\mu$ ; toes  $42$  ( $-47$ ) $\mu$ . Width of lorica at widest part  $78\mu$ , width at anterior points,  $30\mu$ . Depth of ventral sinus  $18\mu$ ; dorsal sinus  $13\mu$ .

*Lepadella whitfordi* was rather common in a freshwater pond on the beach at Morehead City (June 21, 1937). It was also observed in material from Lake Mattamuskeet, and from a freshwater pond at Currituck Sound. It bears some resemblance to *Lepadella xenica*, but differs in a number of details:

<i>Lepadella xenica</i>	<i>Lepadella whitfordi</i>
Shape of lorica distinctly pyriform, widest anteriorly.	Shape ovoid, widest part near middle.
Collar very prominent.	Collar average.
Foot groove suddenly flaring posteriorly.	Foot groove but slightly flaring.
Toes gradually diminishing from base to bristle-like tips.	Toes abruptly diminishing to very long bristle-like tips.
Ventral margins of head opening straight with blunt anterior points.	Ventral margins of head opening convex, with broadly acute divergent points.
Dorsal plate with one ridge.	Dorsal plate with four ridges.

**MONOSTYLA Ehrenberg**

Edmondson (1935) proposed the inclusion of *Monostyla* in the genus *Lecane* as there have been several species described which are definitely transitional between the genera. *Lecane* has two toes, *Monostyla* only one. Several species have been described in which the toes are partly fused. These are interesting evidences of the derivation of *Monostyla* from a *Lecane*-like ancestor, but they should not invalidate the genus

*Monostyla*. There are nearly a hundred species of *Lecane* in which the two toes are distinctly separate, and there are at least forty-five valid species in the genus *Monostyla* which always have the two toes completely fused into one. Combining these two large genera under one inclusive genus would obscure the marked differences between two large groups of species, and would gain little. *Lecane* as previously understood is awkwardly large; why overburden it by including at least forty-five more species that can be easily segregated? From both the point of view of utility (which taxonomy must always take into consideration) and in obscuring the natural relationships and differences between large groups of species, the inclusion of *Monostyla* in *Lecane* is very undesirable.

***Monostyla ornata* Harring and Myers**

Harring and Myers, Trans. Wis. Acad. Sci., Arts, and Lett. 22: 403, pl. 36, figs. 1, 2, 1926.

A few specimens were seen in material from Cathernis Lake (Aug. 12, 1937). This is the second record of this unusually ornamented species for North America.

***Monostyla perplexa* sp. nov. Pl. 7, fig. 4.**

The outline of the lorica is broadly ovate; its width is about two-thirds of the length. The anterior dorsal margin is nearly straight; the ventral margin has a shallow median concavity. No anterior spines are present. The dorsal plate is broadly ovate and somewhat truncate posteriorly. The ventral plate is broadly oval and somewhat narrower than the dorsal plate. The surface markings are limited to a transverse ventral fold a short distance in front of the foot. The lateral sulci are deep. The posterior segment is truncate and rather large, projecting considerably beyond the dorsal plate. The first foot joint is indistinct, the second joint is large and subcircular. The toe is long, nearly one-third of the total length, straight and parallel-sided, terminating in a fairly long claw with two minute, basal spicules.

Total length 120 $\mu$ ; length of dorsal plate 72 $\mu$ , of ventral plate 79 $\mu$ ; width of dorsal plate 67 $\mu$ , of ventral plate 63 $\mu$ ; width of anterior margin 51 $\mu$ ; toe without claw 36 $\mu$ , claw 7 $\mu$ .

*Monostyla perplexa* was rather common in Lake Mattamuskeet. It is closely related to *Monostyla lunaris*, but differs in so many details that I am calling it new. It is smaller in size, has quite different anterior margins, is proportionately much wider at the anterior margin,

and differs in various other details of the lorica. The toe is proportionately shorter and does not narrow near the basal spicules as is usually the case in *Monostyla lunaris*.

***Monostyla tethis* Harring and Myers**

Harring and Myers, Trans. Wis. Acad. Sci., Arts, and Lett. **22**: 405, pl. 38, figs. 1, 2, 1926.

A few specimens observed from a fish pond near Pleasant Garden, N. C. Total length  $92\mu$ , length ventral plate  $69\mu$ , width ventral plate  $57\mu$ , width anterior margin  $45\mu$ , toe and claw  $25\mu$ .

***Monostyla unguitata* Fadeev. Pl. 7, fig. 5.**

Fadeev, Proc. Nat. Soc. Kharkov. **50**(1): 9, fig. 7, 1925.

The outline of the lorica is broadly oval; its width is about four-fifths of the length. The anterior dorsal margin is nearly straight. The ventral margin has a broad, shallow, V-shaped anterior sinus between rather pointed lobes projecting considerably beyond the dorsal plate. The dorsal plate is oval and narrower than the ventral; the ventral plate is more distinctly pyriform than the dorsal and wider; the transverse fold is very strongly marked. The posterior segment is rather small and rounded posteriorly. The first foot joint is indistinct, the second large and subtriangular in form. The toe is fairly long; it is slightly enlarged toward the posterior end; the claws are distinct and quite long. The lorica is ornamented with a pattern of reticular areolations.

Total length  $160\mu$ ; length of dorsal plate  $110\mu$ , of ventral plate  $122\mu$ ; width of dorsal plate  $88\mu$ , of ventral plate  $95\mu$ , of anterior margin  $58\mu$ ; length of toe  $30\mu$ , of claw  $14\mu$ .

*Monostyla unguitata* was collected in a canal at Swindell Fork of Lake Mattamuskeet. The North Carolina forms agree fairly well with Fadeev's figures. The Russian forms are proportionately wider and somewhat smaller in size. The shape of the toes and claws and of the anterior margin is very similar in both localities, and are very distinctive. This species is closely allied to *Monostyla cornuta*.

***Monostyla whitfordi* sp. nov. Pl. 7, figs. 2, 3.**

The outline of the lorica is very broadly reversed-ovate; its width is but little less than the length. The anterior margin of the dorsal plate is about straight or slightly convex; the ventral margin is slightly concave; short anterior spines are present. The dorsal plate is very

broadly oval and rounded posteriorly. The ventral plate is much narrower and oval in outline, and is somewhat flexible. The lorica is without surface markings. The posterior segment is large and rounded; it projects with its entire length below the dorsal plate. The coxae plates are fairly large and obtusely rounded posteriorly.

The first foot joint is indistinct, the second joint fairly large and subsquare, projecting slightly beyond the lorica. The toe is fairly long; it is slightly enlarged toward the posterior end; the claw is fairly long, acutely pointed, and has a median dividing line; two basal spicules are present.

Total length  $124\mu$ ; length of dorsal plate  $76\mu$ , of ventral plate  $88\mu$ ; width of dorsal plate  $69\mu$ , of ventral plate  $59\mu$ , of anterior margin  $50\mu$ ; length of toe without claw  $36\mu$ , claw  $8\mu$ .

*Monostyla whitfordi* was rather common in a collection from Lake Waccamaw (Aug. 10, 1937). It is related to *Monostyla obtusa* and *Monostyla vastita*. It resembles the latter in the general shape of the body, but the toe is very similar to that of *Monostyla obtusa*. It is readily distinguishable from either of these species. I take pleasure in naming this species for Larry A. Whitford, the collector of all the samples on which this report is based.

#### ***Testudinella angulata* Myers. Pl. 8, fig. 4.**

Myers, Am. Mus. Novitates No. 761, p. 1, figs. 1, 2, 1934.

Seen in material from several North Carolina samples. Total length  $133\mu$ ; greatest width  $88\mu$ ; anterior margin  $56\mu$ .

#### ***Testudinella caeca* (Parsons). Pl. 8, figs. 1, 2.**

*Pterodina caeca* Parsons, Jour. Quekett Micro. Club, ser. 2, 4: 379, pl. 25, fig. 3, 1892; Rousselet, ibid. 7: 27, pl. 3, fig. 1, 1898.

*Testudinella caeca* Harring, Bull. U. S. Nat. Mus. 81: 100, 1913; Carlin-Nilsson, Kungl. Fysiogr. Sällsk. Lund Förh. 5 (Nr. 18): 8, fig. 17, 1935; Hauer, Beiträge zur Naturkund. Forsch. Südwestdeutschland 1(1): 147, pl. 1, fig. 1a-c, 1936.

*Testudinella caeca* var. *lermaensis* Ahlstrom, Trans. Am. Micro. Soc. 51: 249, fig. 6, 1932.

Large examples of this species were found in a freshwater pond on the beach at Morehead City. The anterior dorsal margin has but a small, rounded median elevation, and the lateral antennae are exactly marginal. The foot opening is shield-shaped due to an extension of

the ventral plate overhanging the foot opening as a rudimentary foot sheath.

	Canal, Fairfield	Cuscut Creek, Balkhausen	Morehead City
Length.....	137 $\mu$	145 $\mu$	170 $\mu$
Width.....	92 $\mu$	96 $\mu$	112 $\mu$
Anterior points.....	44 $\mu$	50 $\mu$	57 $\mu$

***Testudinella dentata* Myers. Pl. 8, figs. 6, 7.**

Myers, Am. Mus. Novitates No. 761, p. 3, figs. 7, 8, 1934.

Material which is probably referable to this species was collected in freshwater creek, north of Bath. It differs from Myers' description in that the anterior dorsal margin is not notched; the mental margin is more markedly undulate with a wider median sinus; and the body is proportionately much wider. The lorica of the North Carolina form is marked by longitudinal striations, very noticeable along the lateral edges. Total length 127 $\mu$ ; greatest width 102 $\mu$ .

***Testudinella dicella* Myers. Pl. 8, fig. 5.**

Myers, Am. Mus. Novitates No. 761, p. 5, figs. 11, 12, 1934.

The material I have seen of this species from North Carolina and Florida differs in various details from the figure by Myers. The mental margin has a much narrower median sinus, and the rather flexible dorsal margin has an acutely pointed median spine.

	Rollsville	Milbournie Pond (Wake Co.)
Total length.....	153 $\mu$	144 $\mu$
Greatest width.....	75 $\mu$	76 $\mu$
Anterior points.....	50 $\mu$	56 $\mu$

***Testudinella discoidea* sp. nov. Pl. 8, fig. 3.**

The lorica is orbicular in outline. The anterior dorsal is but little elevated if at all, except for a short median spine-like projection. The ventral margin rounds into a rather wide and deep V-shaped central sinus.

The foot opening is wide and shield-shaped in outline; it is terminal or nearly so.

Length of lorica 141 $\mu$ , width of lorica at widest part 127 $\mu$ ; anterior points 60 $\mu$ .

*Testudinella discoidea* was observed in material from Newport and from a ditch with sphagnum near White Lake. I was unable to get

the few specimens seen into position to determine the shape of the transverse section of the body. However, the body is not flexed, is much compressed, and has no ventral ridge. The body is faintly ornamented with longitudinal striations.

*Testudinella discoidea* is not likely to be confused with any other described species. It resembles *Testudinella caeca* in the shape of the foot opening.

**Trichocerca (Diurella) bidens** (Lucks). Pl. 9, figs. 8, 9.

*Diurella bidens* Lucks, Westpr. Botanisch-Zoologischen Verein 1912, p. 66, figs. 12-13; Sachse, Archiv für Hydrobiologie 9: fig. 3, 1914.

*Diurella cavia* Fadeev non Gosse, Proc. Nat. Soc. Kharkov 50(2): 151, pl. 2, fig. 2, 1927.

Harring (1913) considered *Diurella bidens* as a synonym of *Diurella cavia*, and various authors have followed this disposition. However, neither Gosse nor Jennings mentions anterior projections for *D. cavia*: in fact Jennings states, "This species is to be recognized by the very small, plump body, without teeth at the anterior margin of the lorica." *Diurella bidens* has a definite tooth-like projection, quite symmetrically placed, on either side of the head. These cannot be considered mere plaits due to foldings in the head sheath. The head sheath is indistinctly separated from the rest of the lorica, and is provided with several longitudinal plaits at which folding takes place when the head is retracted. The lorica forms an arc on the dorsal side, while the ventral margin is nearly straight. The foot is situated on the ventral surface considerably in front of the posterior end. The two toes are about equal in length.

	<i>Linsville, N. C.</i>	( <i>Lucks</i> )	( <i>Fadeev</i> )
Total length.....	167 $\mu$	170 $\mu$	120-150 $\mu$
Length toes.....	50 $\mu$	55 $\mu$	30- 35 $\mu$

**Trichocerca (Diurella) edmondsoni** Myers. Pl. 9, fig. 2.

*Diurella edmondsoni* Myers, Am. Mus. Novitates No. 830, p. 14, figs. 10, 12, 1936.

This species is readily distinguished by the prominent, projecting plate on the right side of the head. The material from North Carolina had a very distinct dorsal ridge running from the forward side of the head plate to near the posterior end of the lorica. Myers did not find a ridge on material from New Jersey. The right toe is about two-fifths the length of the longer left toe and is exceptionally stout.



Total length  $250\mu$ , length body including foot  $143\mu$ , length left toe  $110\mu$ , right toe  $40\mu$ .

***Trichocerca (Diurella) mucripes* sp. nov.** Pl. 9, fig. 6.

The body is elongate and curved, forming an arc dorsally. The head sheath is distinctly set off from the rest of the lorica, and is marked by a number of longitudinal plaits (probably nine). On the right side the anterior edge bears a prominent tooth. There is an indication of a ridge. The foot is sharply set off from the body, is slender and tapers but little; on the posterior edge is a prominent recurved tooth-like spine. The toes are about equal in length, and about half as long as the body.

Length of body including foot  $126\mu$ , length of toes  $62\mu$ .

This species was collected sparingly in a fish pond near Pleasant Garden, N. C. It is closely related to *Trichocerca tigris* from which it differs in its smaller size and in the possession of the spine-like process on the foot.

***Trichocerca rosea* (Stenroos).** Pl. 9, fig. 5.

Fadeev, Proc. Nat. Soc. Kharkov. **50**(2): 150, pl. 2, fig. 6, 1925; Hauer, Zool. Anz. **94**: 180, fig. 6, 1931; Ahlstrom 1934, Trans. Am. Micro. Soc. **53**: 265; Edmondson, Trans. Am. Micro. Soc. **55**: 220, 1936; Myers, Am. Mus. Novitates No. 903, p. 6, 1937.

*Mastigocerca rosea* Stenroos, Acta Soc. Fauna Flora Fennica **17**: 146, pl. 2, fig. 1, 1898.

*Rattulus roseus* Jennings, Bull. U. S. Fish. Comm. **22**: 341, pl. XV, fig. 137, 1903.

This species has been reported for Florida, Maine, the Adirondack region of New York, and now from North Carolina, and will probably prove to be widely distributed. In material from a canal at Swindell Fork of Lake Mattamuskeet, N. C., the lorica projects backward after the origin of the foot into a definite spine. Specimens measure  $290\mu$  long for body including foot, with the main toe  $190\mu$  long.

***Trichocerca (Diurella) rotundata* Myers.** Pl. 9, fig. 7.

Myers, Am. Mus. Novitates No. 903, p. 13, figs. 13, 16, 20, 1937.

Rather common in material from North Carolina. Specimens measure  $125\mu$  long, with longest toe  $40\mu$  long.

**Trichocerca stylata** (Gosse). Pl. 9, fig. 4.

Harring, Bull. U. S. Nat. Mus. **81**: 105, 1913; Fadeev, Trav. Stat. Biol. du Caucase du Nord **1**(2): 8, figs. 6-8, 1926.

*Monocerca stylata* Gosse, Ann. Mag. Nat. Hist., ser. 2, **8**: 199, 1851.

*Rattulus stylatus* Jennings, Bull. U. S. Fish Comm. **22**: 338, pl. 10, figs. 92-94, 1903.

This species appears to be rather widely distributed. I have seen material from Parahyba, Brazil, Lake Xochimilco near Mexico City, as well as Swannanoa, N. C. The head is always thrown into a large number of plaits; the body is plump and somewhat conical-shaped; the main substyle is usually closely appressed along the short toe, so that its length is indeterminable. Jennings (1903) mentions that it might be as long as one-half the length of the main toe; Fadeev (1926) figures it as being about half as long. It is likely that *Diurella inermis* (Lindl.) is a synonym of this species.

Length of lorica and foot  $170\mu$ , depth  $71\mu$ , toe  $52\mu$ .

**Trichocerca (Diurella) tortuosa** Myers. Pl. 9, fig. 3.

*Diurella tortuosa* Myers, Am. Mus. Novitates No. 830, p. 15, figs. 14, 17, 1936.

The material from Rockfish, North Carolina, has the lorica but little twisted, and is rather straight on the ventral surface. However, it is obviously referable to this species.

Length body including foot  $156\mu$ , length left toe  $80\mu$ , right toe  $38\mu$ .

LOS ANGELES, CAL.

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## PLATE 6

- Fig. 1. *Colurella mucronulata* sp. nov., lateral view.
- Fig. 2. *Colurella mucronulata* sp. nov., ventral view.
- Fig. 3. *Colurella hindenburgi* Steinecke, lateral view.

- Fig. 4. *Colurella hindenburgi* Steenecke, dorsal view.  
Fig. 5. *Colurella sulcata* (Stenroos), lateral view.  
Fig. 6. *Lepadella dactyliseta* (Stenroos), ventral view.  
Fig. 7. *Lepadella whitfordi* sp. nov., ventral view.  
Fig. 8. *Lepadella whitfordi* sp. nov., dorsal view.  
Fig. 9. *Lepadella rhomboides* (Gosse), dorsal view.  
Fig. 10. *Lepadella akrobeles* Myers, dorsal view.  
Fig. 11. *Lepadella whitfordi* sp. nov., cross section of body.  
Fig. 12. *Lepadella akrobeles* Myers, cross section of body.  
Fig. 13. *Lepadella quadricarinata* (Stenroos), dorsal view.

## PLATE 7

- Fig. 1. *Lecane luna* var. *presumpta* nov. var., ventral view.  
Fig. 2. *Monostyla whitfordi* sp. nov., dorsal view.  
Fig. 3. *Monostyla whitfordi* sp. nov., ventral view.  
Fig. 4. *Monostyla perplexa* sp. nov., ventral view.  
Fig. 5. *Monostyla unguitata* Fadeev, ventral view.  
Fig. 6. *Monostyla cornuta* (Müller), ventral view.  
Fig. 7. *Conochiloides coenobasis* Skorikov, lateral view.  
Fig. 8. *Conochiloides exiguus* sp. nov., lateral view; specimen partly contracted.  
Fig. 9. *Conochiloides coenobasis* Skorikov, trophi.  
Fig. 10. *Conochiloides natans* (Seligo), trophi.  
Fig. 11. *Conochiloides exiguus* sp. nov., trophi.  
Fig. 12. *Conochiloides dossuarius* (Hudson), trophi (based upon a sketch furnished by Frank J. Myers).

## PLATE 8

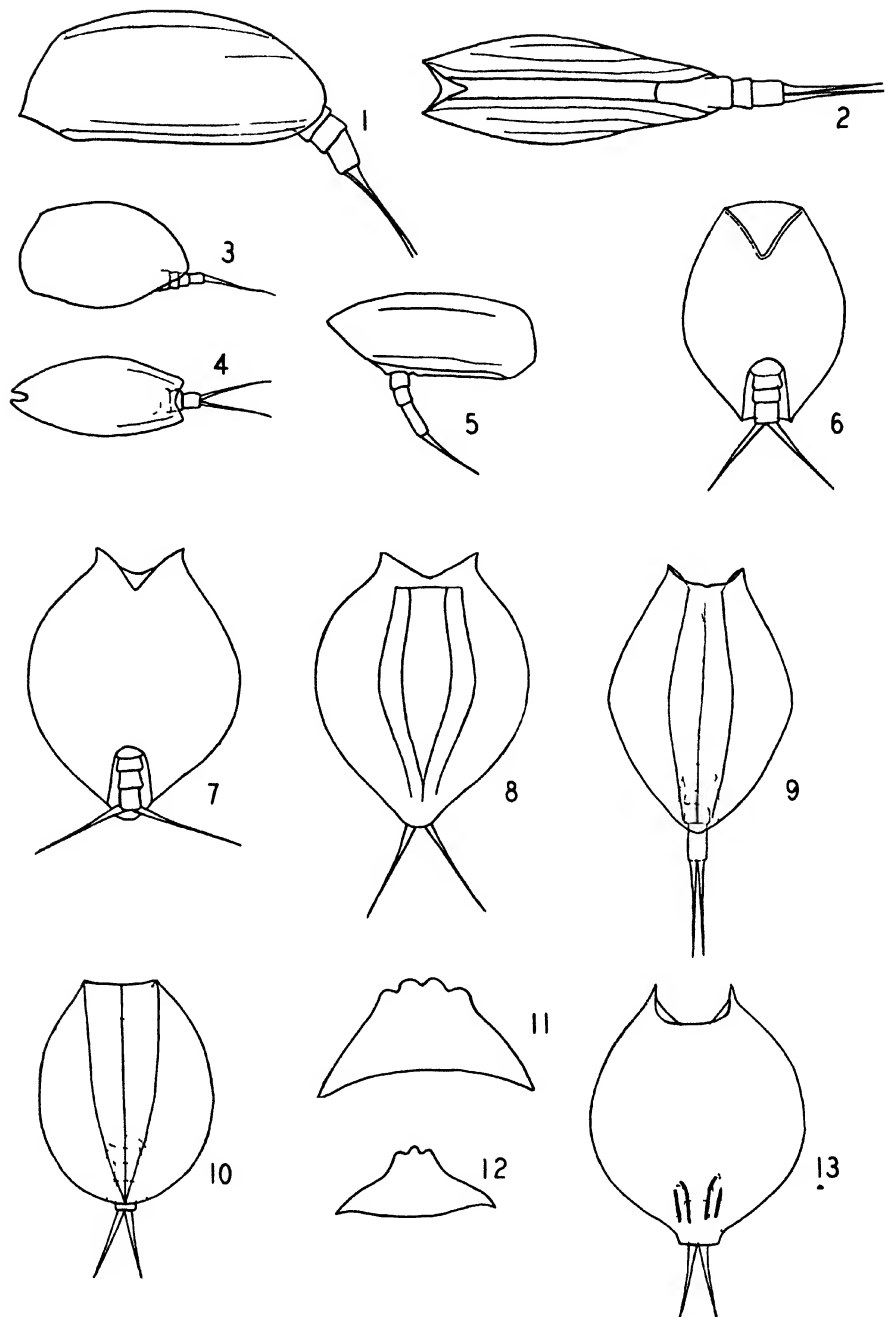
- Fig. 1. *Testudinella caeca* (Parsons), ventral view, specimen from Cucold Creek, Belhaven.  
Fig. 2. *Testudinella caeca* (Parsons), ventral view, specimen from pool at Morehead City.  
Fig. 3. *Testudinella discoidea* sp. nov., ventral view.  
Fig. 4. *Testudinella angulata* Myers, ventral view.  
Fig. 5. *Testudinella dicella* Myers, ventral view.  
Fig. 6. *Testudinella dentata* Myers, ventral view.  
Fig. 7. *Testudinella dentata* Myers, lateral view.  
Fig. 8. *Testudinella parva* (Ternetz), ventral view.  
Fig. 9. *Testudinella incisa* (Ternetz), ventral view.  
Fig. 10. *Testudinella reflexa* (Gosse), ventral view.  
Fig. 11. *Testudinella parva* var. *bidentata* (Ternetz), ventral view.

## PLATE 9

- Fig. 1. *Kellicottia bostoniensis* (Rousselet), dorsal view.  
Fig. 2. *Trichocerca edmondsoni* Myers, lateral view.  
Fig. 3. *Trichocerca tortuosa* Myers, lateral view.  
Fig. 4. *Trichocerca stylata* (Gosse), lateral view.

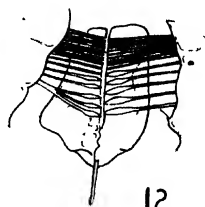
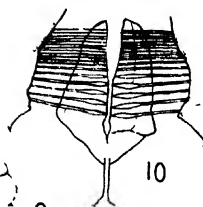
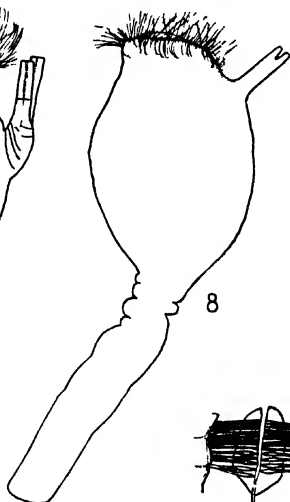
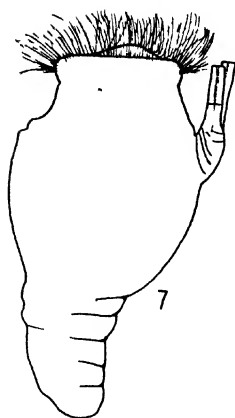
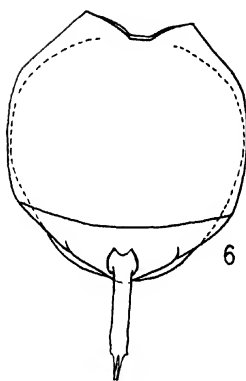
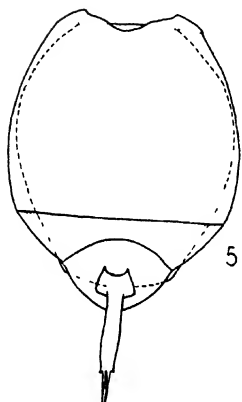
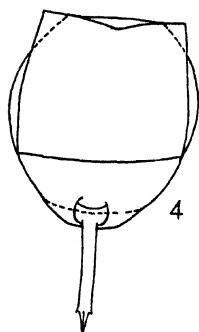
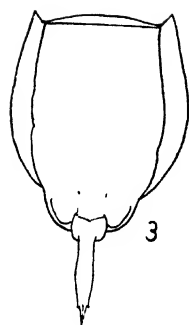
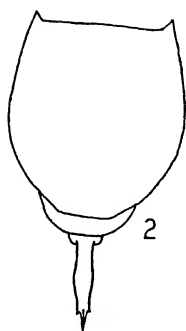
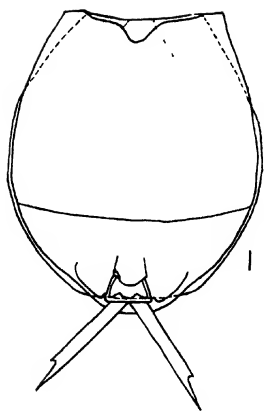
- Fig. 5. *Trichocerca rosea* (Stenroos), lateral view. .  
Fig. 6. *Trichocerca mucripes* sp. nov., lateral view.  
Fig. 7. *Trichocerca rotundata* Myers, lateral view.  
Fig. 8. *Trichocerca bidens* (Lucks), lateral view.  
Fig. 9. *Trichocerca bidens* (Lucks), view of head sheath from above.

# PLATE 6



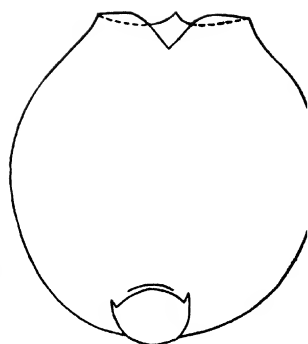
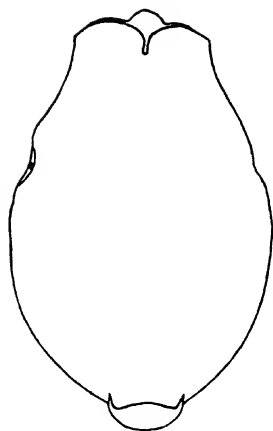
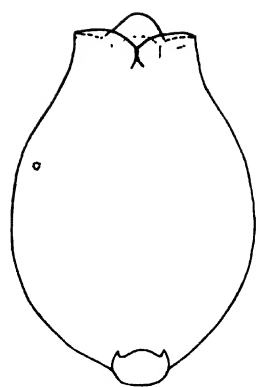


# PLATE 7

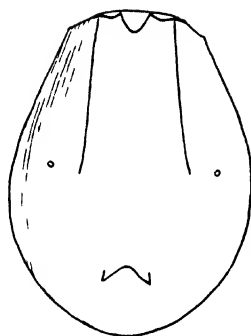




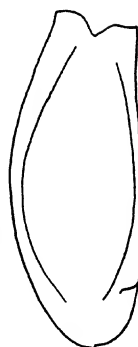




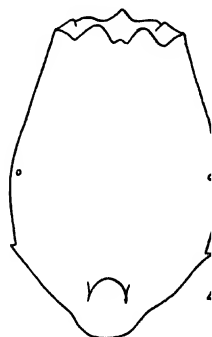
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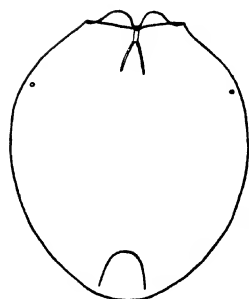
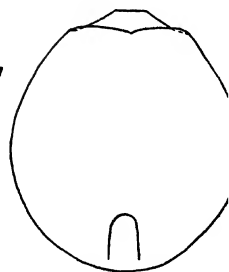
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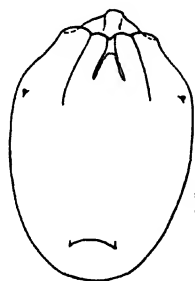
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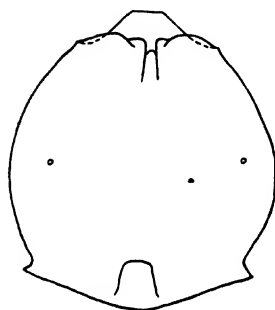
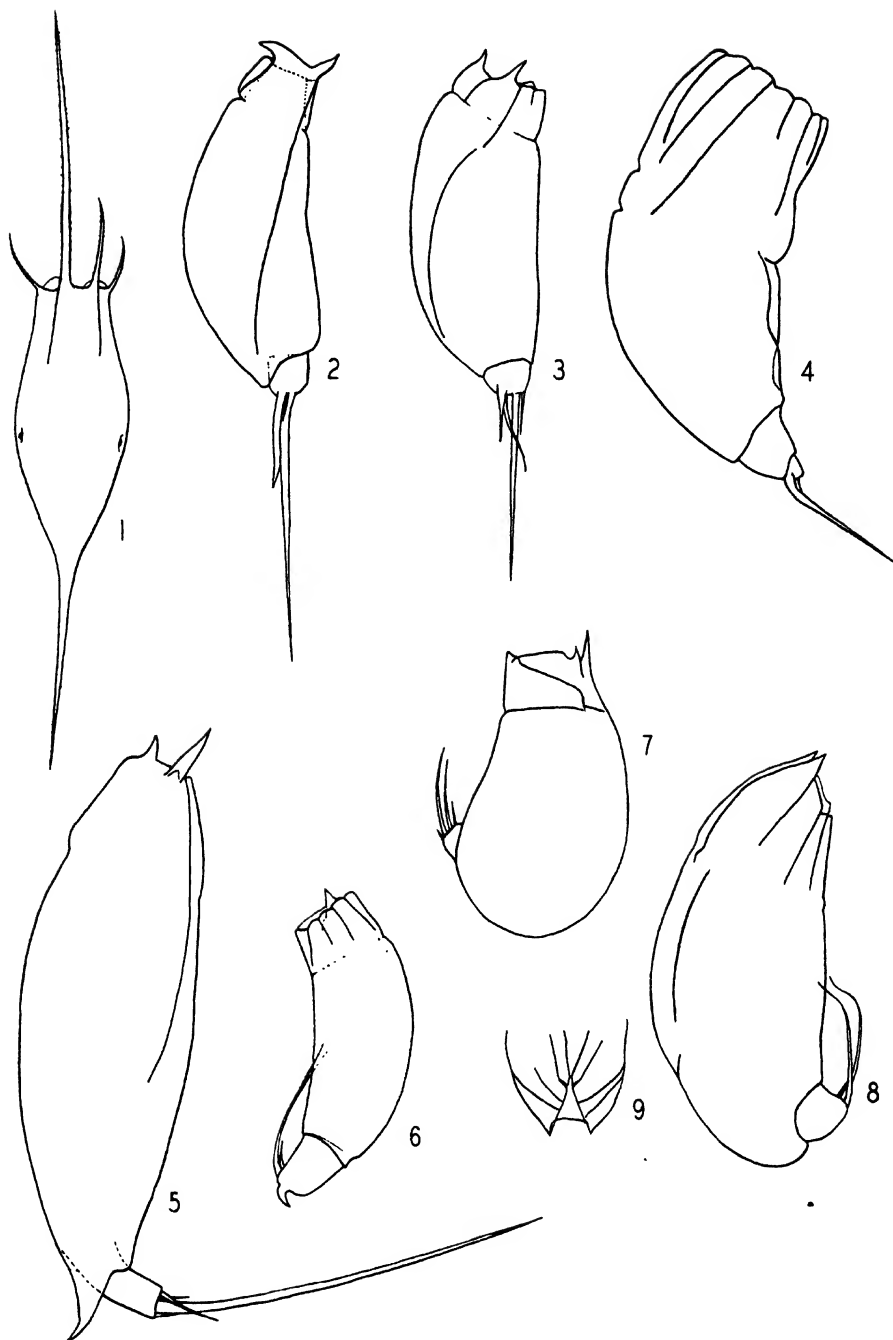




PLATE 9





# STRUCTURE AND DIVISION IN THE ASTOMATOUS CILIATE METARADIOPHRYA ASYMMETRICA N. SP.

By C. DALE BEERS

PLATES 10 AND 11

## INTRODUCTION

The genus *Metaradiophrya* was established by Heidenreich (1935) to receive two well-known species of *Hoplitophrya* Stein, 1860, which differ significantly from other members of the genus. These are *H. lumbrici*, which was described originally as *Opalina lumbrici* by Dujardin (1841), and *H. falcifera* Stein, 1861. As a result of this division, *Hoplitophrya* now embraces slender, elongate, astomatous infusoria which have dorsally a single longitudinal row of from 15 to 30 contractile vacuoles and ventrally in the mid-line a single spicule bearing at its anterior end a small, pointed tooth; whereas *Metaradiophrya* embraces shorter and broader astomatous forms which have laterally two rows of a few contractile vacuoles each and anteriorly for attachment a hook with which is associated a system of ectoplasmic supporting fibers. Both genera inhabit the alimentary tract of oligochaetes.

Reference may be made to the studies of Cheissin (1930) and Heidenreich (1935) for details of classification in the group Astomata. Their work has done much to alleviate the taxonomic confusion occasioned by the inadequate descriptions of earlier investigators, as well as by the absence in these ciliates of a mouth and associated feeding organelles—structures of primary importance in the classification of infusoria. It will suffice to state that Cheissin (1930, p. 605) united in the Hoplitophryidae all Astomata that possess conspicuously differentiated skeletal elements, whether in the form of a hook-like organ of attachment or a system of supporting fibers or both, and that Heidenreich recognizes in the Hoplitophryidae eight genera, one of which is *Metaradiophrya*. Heidenreich (p. 335 and p. 338) gives the complete synonymy of *M. lumbrici* and *M. falcifera*.

Since the specimens of *Metaradiophrya* that I have found in the intestine of the earthworm *Eisenia lönnbergi* do not agree with the descriptions of either of the two known species as regards the arrange-

ment of the skeletal elements and the structure of the micronucleus, I shall designate them as *Metaradiophrya asymmetrica* n. sp., because of the asymmetrical arrangement of the skeletal elements. Unfortunately, I have had no opportunity to examine specimens of *lumbrici* and *falcifera*.

#### SOURCE OF MATERIAL; METHODS; INCIDENCE OF INFECTION

The worms from which the ciliates were taken agree with Smith's description (1917, p. 164) of *Helodrilus (Eisenia) lönnbergi* (Michaelsen) as regards all important diagnostic features except the position of the first dorsal pore. According to Smith, it is found in intersegmental groove 7/8; in the specimens that I have examined it occurs in 4/5, but this difference is no doubt one of subspecific import. Stephenson (1930, p. 908) calls attention to the inconvenience of designating the common Lumbricids by generic, subgeneric and specific names and considers the subgenera under *Helodrilus* as independent genera. Following his practice, I am designating the host as *Eisenia lönnbergi*.

To obtain ciliates for study, the worms were narcotized in 1% chlore-tone in 10% alcohol, rinsed thoroughly under the tap and rolled on filter paper to remove the excess water. Next, they were opened by a longitudinal incision in the body wall and were pinned out on sheet cork. Finally, the intestine was opened and portions of the contents were removed by means of a small wooden spatula to large drops of distilled water in depression slides. From these the ciliates were transferred to micro slides by means of a small pipette. Dilution of the intestinal contents with distilled water was much less harmful to the ciliates than dilution with any of a number of inorganic salt solutions that were tried.

Permanent whole mounts were made by attaching fixed specimens to slides with celloidin before staining (Aunap, 1927). Sections were prepared by transferring the fixed specimens to a small bag made of cat mesentery (Beers, 1937).

The immersion of the hosts in chlore-tone had no observably injurious effect on the ciliates, for specimens removed from active worms lived no longer outside their host than those from narcotized worms, nor did the two groups differ in shape, structure or behavior. Early attempts to remove the ciliates from normal, active worms proved unsatisfactory and exasperating, since such worms, when pinned out, invariably tore themselves into contracted fragments. This practice was discontinued as soon as the relative harmlessness of the chlore-tone procedure was established, though special precautions—the rinsing and drying treatment already mentioned—were taken to prevent either the chlore-tone or tap water from coming in contact with the ciliates.

Unfortunately, I have found as yet no medium in which *Metaradiophrya* will live for any appreciable length of time outside of its host. Indeed, it proved to be somewhat difficult to ascertain, with the desired degree of accuracy, the normal dimensions of the ciliate—the dorso-ventral one in particular—for the animals swell rapidly after removal from their host. I hesitate to attribute this to oxygen toxicity—the usual explanation—until the probable chemical and physical inadequacies of the media have been evaluated. Specimens examined in coelomic fluid of the earthworm showed least swelling and lived longest. Further attempts are in progress to determine the cultural needs of the ciliates.

More than 400 adult specimens of *Eisenia lönnbergi* from the environs of Chapel Hill were examined for *Metaradiophrya*. Approximately 60% of them were infected, but not heavily. As a rule, only five to ten ciliates could be found in an infected host. Undoubtedly some were overlooked, for most of them seemed to be closely applied to the lining epithelium of the intestine. Often when the contents appeared to be negative or to contain only a ciliate or two, the examination of scrapings from the intestinal lining showed numbers to be present. Six worms were exceptions, in that each contained at least 150 specimens; these six hosts furnished nearly all of the division stages that were found. If the intestine is thought of as consisting of three parts, fully 90% of the specimens of *Metaradiophrya* were found in the middle third, with the remaining few in the posterior part of the anterior third. Neither conjugation nor encystment was observed. I can offer no satisfactory comment on the method of transmission from host to host.

It may be mentioned at this point that of the 400 worms examined, fully 80% were infected with another intestinal ciliate, a species of *Hysteroecinetes* Diesing, 1866, which is probably known better under the synonym *Ladopsis* Cheissin, 1928. This form, like its near relative, *Ptychostomum*, is remarkable in having the mouth at the extreme posterior end of the body. A study of its structure and division is now in progress. Approximately 50% of the 400 worms harbored both *Metaradiophrya* and *Hysteroecinetes*, but the two ciliates were rarely found in the same region of the intestine. In general, *Hysteroecinetes* occupied a region posterior to that inhabited by *Metaradiophrya*.

A further point concerning the occurrence of the two ciliates is of interest. A species of the earthworm *Pheretima* measuring up to 20 cm. in length was always found along with the specimens of *Eisenia*. Yet the examination of 110 specimens of *Pheretima* failed to disclose a single ciliate. Whether this indicates a high degree of host specificity



in the ciliates or results merely from the inability of the infective stages to pass unharmed through the more powerful gizzard of *Pheretima* is not clear.

METARADIOPHRYA ASYMMETRICA N. SP.; DESCRIPTION; COMPARISONS WITH  
M. LUMBRICI AND M. FALCIFERA

*Shape and size.* The shape of *Metaradiophrya asymmetrica* permits for descriptive purposes the use of the topographic terms usually applied to bilaterally symmetrical animals. Dorsal and ventral surfaces are clearly differentiated. The dorsal surface is somewhat convex and the ventral surface, on which is found a hook for attachment to the intestinal epithelium, is in general flattened or slightly concave (figs. 2 and 3). The animal as a whole is dorso-ventrally flattened, but its dorso-ventral dimensions vary in different regions of the body. It is thinnest at the posterior end (figs. 2, 3, and 12) and increases in thickness as the anterior end is approached until the region of the attachment organelle is reached; here there is a rather sudden decrease in thickness to produce on the antero-ventral surface an excavation or depression (fig. 2, D) along the right margin of which lies the shaft (S) of the hook (H). The anterior end of the cell body is rounded, while the posterior end is either rounded or, more commonly, truncated. Often the truncation is oblique, so that the right lateral margin is slightly longer than the left (fig. 1, ventral view of adult individual). The cell body is non-contractile and but slightly flexible. Adult specimens measure 115–150 $\mu$  in length and 55–70 $\mu$  in width.

A relatively thin layer of hyaline ectoplasm is clearly differentiated from an inner region of finely granular endoplasm (figs. 2 and 4, the latter a cross section).

In size *M. asymmetrica* shows no significant differences from *M. lumbrici* and *M. falcifera*. Cépède (1910, p. 401) reports that *Hoplitophrya hamata* Cépède (= *M. lumbrici*) from *Lumbricus terrestris* and *L. rubellus* measures 135 $\mu$  by 66 $\mu$  and Heidenreich's specimens (p. 338) from *L. rubellus* and *Eisenia foetida* measure 120–140 $\mu$  by 60–70 $\mu$ . According to Cépède (p. 405), the largest specimens of *Hoplitophrya falcifera* (= *M. falcifera*) measure 125 $\mu$  by 85 $\mu$ , whereas those found by Heidenreich (p. 338) in *L. terrestris* measure 120–150 $\mu$  by 70–90 $\mu$ .

The three species are also in close agreement regarding the general shape of the cell body. They are all flattened dorso-ventrally and have rounded anterior borders. The posterior border of *lumbrici* is truncated (Cépède, p. 400) as in *asymmetrica*, though it is more rounded in *falcifera*, so that the general cell outline is oval or elliptical (Cépède, p. 405).

Cépède in his description of *lumbrici* (p. 400 and p. 557) makes no mention of an antero-ventral depression; presumably it is present. However, he describes and figures a depression in *falcifera* (p. 407 and Pl. 9, fig. 2) and regards it as having a suctorial function. In *asymmetrica* I have been quite unable to adduce any evidence indicating that this region functions as a sucker. It shows no marginal ectoplasmic thickening (fig. 4) such as would be expected were its function suctorial and it is everywhere provided with cilia which would surely interfere seriously with any suctorial action.

**Macronucleus:** A slender, cylindrical macronucleus lies in the mid-line of the body (fig. 1). In general, it is straight, though in some specimens it shows wide undulations in the sagittal plane (fig. 2). In adult specimens it is at least  $100\mu$  long and  $5-7\mu$  in diameter. With nuclear dyes it shows a lightly staining matrix in which are embedded irregular, closely packed, deeply staining chromatin granules (fig. 15). The macronuclei of *lumbrici* and *falcifera* are of this same type and have been described and figured by Stein (1854, 1861) and Cépède.

**Micronucleus:** The single micronucleus is vesicular and has a diameter of  $3.5-5\mu$ . It is found always well to the right of the macronucleus and just within the posterior half of the cytoplasm (fig. 1). It contains a single, spherical, central karyosome which stains intensely with haematoxylin or acid fuchsin and has a diameter of  $2-2.5\mu$ . Clearly the karyosome contains all of the chromatin, for between it and the nuclear membrane there is only a clear space about  $1\mu$  across. In well stained preparations the micronucleus is quite conspicuous.

This type of micronucleus is very different from that described in *lumbrici* and *falcifera*. In *lumbrici*, according to Cépède (p. 403), it is a small fusiform body measuring only  $5\mu$  by  $1.3\mu$ . His figure (Pl. 11, fig. 26) shows it as a very inconspicuous structure quite near the ectoplasm of the left side of the cell. In *falcifera*, according to Stein (1861) and Cépède (p. 407), the micronucleus is likewise a small ovoidal body. Neither Cépède (Pl. 9, fig. 3 of *falcifera*) nor Stein (1854, Pl. 5, fig. 24 of *lumbrici*) shows the micronucleus in figures of dividing specimens. Evidently it is an inconspicuous structure in these two species.

**Skeletal elements:** Undoubtedly the skeletal elements are the structures of greatest interest in *M. asymmetrica*. They consist of a rigid, hook-like organelle of attachment, which is probably chitinous, and of a system of supporting fibers. The attachment organelle consists of a slightly bent shaft which is firmly embedded in the ectoplasm of the antero-dextral margin of the cell body (figs. 1 and 2, S) and is continued anteriorly as a short, stout, sharply pointed hook (H). The hook lies

in the mid-ventral line with its apex directed ventro-posteriorly. I have been quite unable to identify either in the living animal or in stained whole mounts and sections any myonemes for moving the hook. Neither have I been able to observe in living specimens any movement of the hook or any evidence of an articulation between hook and shaft. The shaft is about  $30\mu$  long and  $2\mu$  in diameter; the hook is about  $10\mu$  long.

The supporting fibers ("Skelettstrahlen") are found in the ectoplasm of the ventral surface (fig. 1, F and TF). In general, their course is longitudinal and they are restricted to the depressed antero-ventral surface. They lie just beneath the longitudinal rows of cilia and parallel to them. In living specimens they may be mistaken easily for continuations of the ciliary rows. Only in suitably stained preparations can their size, arrangement and extent be clearly ascertained. With iron haematoxylin following Schaudinn or Bouin fixation they stain intensely black, as do the hook and shaft. With Mallory's stain these structures are colored a brilliant red, whereas they scarcely stain at all in Delafield's haematoxylin.

The fibers do not have a bilaterally symmetrical arrangement. Those of the left half of the antero-ventral surface (fig. 1, F) arise in the mid-line near the base of the hook and diverge slightly in passing sinistro-posteriorly. The fibers lying to the right of the mid-line originate near the shaft and continue directly backward. There are from 25 to 30 fibers in this entire group. They are spaced at intervals of  $1\mu$  and they become progressively shorter from left to right across the depression. All of them originate dorsal to the shaft. The longest ones measure  $40\mu$  in length, the shortest ones about  $7\mu$ . Proceeding toward the right, there follows an area embracing six to eight rows of cilia that is quite devoid of fibers (fig. 1, AF). Finally, there is a tuft of from seven to nine fibers along the right margin of the depression (fig. 1, TF). These originate near the end of the shaft and, diverging slightly, continue posteriorly for 5- $10\mu$ .

The superficial position of the fibers and their appearance when viewed transversely are shown in fig. 4 (section of a specimen in which the macronucleus extended farther forward than in fig. 1; through the larger group of fibers). The fibers (F) are elliptical or oval in cross section. They lie in the ectoplasm (EC) very near the external surface, as does the shaft (S) of the hook also. Basal granules cannot be identified with certainty in my sections of the fibers, though cilia are invariably present in this region. Evidently the fibers lie directly beneath

the rows of granules and so near them that the two systems cannot be differentiated. Similar fibers in *Radiophrya tubificis* are likewise oval in cross section and parallel to the ciliary rows, but they lie at the side of the rows, not directly beneath them, according to Rossolimo and Perzewa (1929). The fibers of *Metaradiophrya* no doubt give rigidity to the anterior end of the organism and are therefore to be looked on as supporting elements.

A consideration of the arrangement of skeletal elements in the related genus *Radiophrya* is appropriate at this point. In *Radiophrya*, according to Rossolimo (1926), they consist essentially of a bilaterally symmetrical V-shaped piece ("Pfeilspitze"), the apex of which lies anteriorly in the mid-line and points forward, and of a number of supporting fibers which begin in the V-piece and continue backward in the ectoplasm of the ventral surface. In *R. prolifera* from the oligochaete *Styloscolex baikalensis* and in *R. tubificis* from *Tubifex tubifex* the skeletal elements are of the foregoing type and evidently lend rigidity to the anterior end (Rossolimo, 1926; Rossolimo and Perzewa, 1929), whereas in *R. hophites* a tooth is articulated with the apex of the V-piece (Rossolimo, 1926; Cheissin, 1930, p. 560). Heidenreich, correctly it would seem, regards this arrangement as the underlying plan from which the skeletal elements of *Metaradiophrya* may be readily derived. His observations on *falcifera* show that a V-shaped skeletal piece is present anteriorly, but it is asymmetrical; the left half is slender, elongated and curved; the right, short and relatively thick. A hook ("Haken") is present at the apex of the V-piece and a system of parallel supporting fibers continue posteriorly from the halves of the V. The hook is articulated with the V-piece and may be moved by a bundle of myonemes that lie parallel to the slender half of the V. The *Radiophrya* plan is departed from only as regards the asymmetry of the V-piece.

The skeletal arrangement in *lumbrici* is as follows, according to Heidenreich: The left half of the V-piece is absent, so that the attachment organelle consists only of a hook which is articulated with the slightly bent right half of the V-piece ("Grundstück" of Stein, 1854, p. 184). But the ectoplasmic supporting fibers of the left half originate along the left antero-lateral margin of the cell quite as if the missing half of the V-piece were present! Those of the right side originate along the shaft with which the hook articulates. A group of stout myonemes for moving the hook occupies the position of the missing half of the V-piece; these are the structures that were evidently mistaken by Stein (1854) for a fold along the left antero-lateral margin.

In *M. asymmetrica* the *Radiophrya* plan has undergone further changes. The hook, as said, is immovably fused with the shaft, which appears to be the equivalent of the right half of the V-piece, the left half of which is absent. Myonemes for moving the hook are absent. The supporting fibers of the left side converge anteriorly and bend to the right, so that all of the fibers arise from the right side along the right half of the V-piece. A small area on the right side is devoid of fibers and a group of fibers arises at the posterior end of the shaft. The fibers generally are distinctly shorter than those of *falcifera* and *lumbrici*, to judge by Heidenreich's figures.

These characteristic features of the skeletal elements, together with the vesicular structure of the micronucleus, seem adequate to warrant the description of my specimens from *Eisenia* as a new species.

*Ciliation:* *M. asymmetrica*, like other Astomata, is powerfully ciliated. The cilia are arranged in from 100 to 120 longitudinal rows which are spaced at intervals of  $1\mu$  around the body. As regards their origin anteriorly, the rows, like the supporting fibers, show an asymmetrical arrangement, in that all of them, whether on the dorsal or ventral surface, begin along the right anterior margin of the cell body near the shaft of the hook (figs. 1 and 2). Hence, all the rows of the left half of the body surface diverge from the mid-line near the base of the hook, as do the fibers of the left side. The origin of the dorsal and lateral rows of the right side is shown clearly in figure 2. Posteriorly, the dorsal and ventral rows show little or no convergence toward the mid-line, but end independently along the truncated posterior border (fig. 1). In general, the cilia measure  $7\mu$  in length, but those at the posterior end attain a length of  $10\mu$ , while those of the antero-ventral depression are only 4 to  $5\mu$  long. The ciliate, upon removal from its host, sometimes swims freely and spirals counterclockwise, but more commonly it creeps continuously along the substratum.

*Vacuoles:* In the cytoplasm of each lateral half of *M. asymmetrica*, there is a longitudinal row of from 3-6 vacuoles (figs. 1 and 7-11). Four seems to be the usual number. They lie dorsally in the endoplasm, but very near the ectoplasm (fig. 2). They are not always spaced at regular intervals in the row and sometimes their arrangement into rows is seriously disturbed. Some variations in their arrangement are shown in figures 7-11. In structure and position they resemble contractile vacuoles. In a few specimens, examined in earthworm coelomic fluid, I have observed incomplete and independent contractions of some of the vacuoles, but in intestinal contents diluted with distilled

water, Knop solution, Locke's solution and other fluids I have never observed their contraction. No doubt their failure to contract is the result of the unfavorable conditions of observation, and I have no doubt that under normal and favorable conditions of life they are contractile. Similar vacuoles occur in *lumbrici* and *falcifera*; Cépède (p. 402) describes their contraction in *lumbrici*, mentioning in particular their lack of synchronism, but he does not describe their contraction in *falcifera*.

"Silver line system." Treatment with silver nitrate employing the methods of Klein (1926) and Gelei (1935), reveals a "silver line system" (fig. 5) which recalls that of *Paramecium* (Klein, 1926a). The basal granules (BG) of each row are connected by a longitudinal fibril (LF), the function of which is probably conductile. There is also a system of polygons (P), which recall Klein's "indirectly connected" conductile system in *Paramecium*, although the polygons are less regular in outline than in *Paramecium* and the number of basal granules to each polygon varies. Lund (1933) has shown that the outlines of the polygons in *Paramecium* are merely pellicular ridges, not fibrillae, and that each polygonal area is a pellicular depression with a single cilium at its center. I am of the opinion that the polygons of *Metaradiophrya* are likewise pellicular differentiations, since relief staining with nigrosin shows areas that seem to correspond to the polygons of the silver method.

#### DIVISION IN METARADIOPHYRYA ASYMMETRICA N. SP.

The fact that the process of division has never been completely described to my knowledge in *Metaradiophrya* seems to warrant the following somewhat detailed account.

In *M. asymmetrica* fission is transverse but unequal. The plane of division first appears between the posterior and middle thirds of the cell body (fig. 6). (A similar position of the fission plane is shown in Heidenreich's single figure of division in *lumbrici*—Pl. 7, fig. 11.) In the early stages the anterior daughter cell or primate is, therefore, twice as long as the posterior cell or satellite. In volume it is more than twice as large, in view of the thinness of the satellite as measured dorso-ventrally (fig. 12). While the fission plane is being established in the cytoplasm, the karyosome becomes spindle-shaped and stains less intensely (fig. 6), but there is never a dissolution of the micronuclear membrane during division.

Soon the karyosome becomes resolved into a myriad of chromatin

granules within the enlarged and slightly ellipsoidal nuclear membrane. The granules are shown in figures 7 and 13 at the equator of the division spindle. Undoubtedly they are valid chromosomes, some of which appear to be rod-shaped, but attempts to count them were of no avail because of their small size and great numbers. At this stage of division (metaphase), the cytoplasmic constriction deepens, but the macronucleus shows no evidence of division (fig. 7). The micronucleus measures about  $8.5\mu$  by  $7\mu$ .

Next, the chromosomes begin to migrate to opposite ends of the spindle and a slight constriction appears in the macronucleus (figs. 8 and 14). When the chromosomes arrive at the ends of the spindle, they lose their identity by assembling in a spherical mass which soon will be the compact karyosome of the resting micronucleus (figs. 9 and 15). In the meantime the micronuclear membrane pinches in two, the spindle disappears and the cytoplasmic and macronuclear constrictions deepen (fig. 9). Then the macronucleus pinches in two and the original resting condition of the micronucleus is restored (fig. 10). The developing hook (DH) of the satellite appears in the ectoplasm at the extreme anterior end of the cell, but the satellite still remains attached to the primite.

Finally, when the hook and supporting fibers attain their full development in the satellite, the thin cytoplasmic connection between the two daughter cells is severed and they separate. The condition just before their separation is shown in figure 11.

The conditions illustrated in figures 10 and 11 apparently persist for many hours, for relatively little difficulty is experienced in finding late division stages. On the other hand, the stages shown in figures 6-9 are evidently passed through rapidly, for they were found only after long-continued search through many scores of hosts. Should the satellite separate from the primite before its attachment hook is fully developed and presumably before its thigmotactic responses are established, it would surely be swept out of its host to perish. Therefore, the primite retains the original attachment hook and supporting fibers without change during division, while the satellite remains attached until it acquires a fully developed hook. It grows in the meantime and upon separation nearly equals the primite in size.

The fact that the satellite continues to grow throughout the entire division process is evident from an inspection of figures 6-11, which are drawn to the same scale, but it is even more evident when actual dimensions are considered. For example in the dividing specimen of figure

6 the primite measured  $114\mu$  in length, the satellite,  $61\mu$ ; the ratio of primite length to satellite length was, therefore,  $114:61$ , or in simpler terms,  $2:1.07$ . An inspection of figure 12, which shows a fixed unmounted dividing individual in side view, shows that here too the primite had twice the length of the satellite. In the metaphase shown in figure 7, the ratio was  $108:65 = 2:1.12$ ; i.e., the satellite was relatively longer. In figure 8 (anaphase), it was  $102:63 = 2:1.23$ ; in figure 9 (late anaphase), it was  $102:72 = 2:1.41$ ; in figure 10,  $88:74 = 2:1.68$ ; and in figure 11,  $86:78 = 2:1.88$ . This series of measurements made from six different individuals is misleading in one respect; it suggests a decrease in size in the primite as division proceeds. This apparent decrease is merely an accidental result of the chance selection of the series of specimens to be drawn. In reality, dividing specimens vary greatly in length, and the primite in different specimens in the late stages of division (similar to fig. 11) may vary from  $80$ – $120\mu$  in length, the satellite from  $75$ – $110\mu$ .

#### DIAGNOSIS

##### Genus *Metaradiophrya* Heidenreich, 1935

The following enumeration of the characters of the genus is based on original observations on one species and on the published descriptions of the two remaining species. It is given here in order to amplify the somewhat incomplete description furnished by Heidenreich.

Astomatous ciliates (Family Hoplitophryidae) occurring in the intestine of Lumbricidae. Body dorso-ventrally flattened; anterior end rounded; posterior end rounded or truncate; lateral margins parallel; dorsal surface slightly convex, ventral surface flattened or slightly concave; with a depression in the antero-ventral surface the suckorial function of which is questionable. Length,  $115$ – $150\mu$ ; width,  $55$ – $70\mu$ . Macronucleus: Median, elongate, cylindrical; dimensions,  $100\mu$  by  $7\mu$ . Micronucleus: Fusiform, ovoidal or spherical; well to right of macronucleus. Skeletal elements: Anteriorly in the mid-ventral line a chitinous hook for attachment; hook articulated with or fused with a chitinous shaft in the ectoplasm of the right anterior margin or with a similar shaft bearing a slender extension along the left anterior margin; in the ectoplasm of the antero-ventral surface, a system of longitudinal supporting fibers. Contractile vacuoles: Two longitudinal rows of about four vacuoles each; located dorsally between macronucleus and lateral margins of cell; vacuoles feebly contractile or non-contractile. Ciliation: Uniform, dense, powerful; cilia in longitudinal rows spaced at intervals of  $1\mu$  around the body. Reproduction by transverse



unequal fission, the anterior daughter cell being larger than the posterior. Hosts: *Lumbricus terrestris*, *L. rubellus*, *Eisenia foetida* and *Allolobophora caliginosa* (Europe); *Eisenia lönnbergi* (U. S. A.).

Three species.

***Metaradiophrya asymmetrica* n. sp.**

*Micronucleus*: Spherical, vesicular; diameter  $3.5-5\mu$ ; with a compact central karyosome measuring  $2-2.5\mu$  in diameter and containing all of the chromatin; located well to right of macronucleus just within the posterior half of cell body. *Attachment hook*: Anteriorly in the mid-ventral line a posteriorly directed chitinous hook for attachment; length,  $10\mu$ ; hook continued into a chitinous shaft in ectoplasm of right antero-lateral margin; dimensions of shaft,  $25-30\mu$  by  $2\mu$ ; hook immovably anchored in ectoplasm by shaft; myonemes absent. *Supporting fibers*: In the ectoplasm of the depressed antero-ventral surface a group of 25-30 longitudinal fibers, all of which arise from the right antero-lateral margin along the shaft of the hook. Most of them proceed toward the left, then posteriorly; they decrease in length from left to right ( $40\mu-7\mu$ ) across the depression. With an area devoid of fibers in the right half of the depression; with a group of 7-9 short fibers that continue posteriorly from the end of the chitinous shaft. *Habitat*: Middle third of the intestine of the earthworm *Eisenia lönnbergi*.

*Metaradiophrya asymmetrica* differs from *M. lumbrici* (Dujardin) and *M. falcifera* (Stein) with respect to the structure of the micronucleus and the arrangement of the skeletal elements (attachment hook and supporting fibers). In *lumbrici* and *falcifera* the micronucleus is fusiform or ellipsoidal and compact, and the hook is articulated with its shaft so that it may be moved by special myonemes. In *falcifera* the stout shaft of the right side is continued as a slender rod along the left antero-lateral margin. In *lumbrici* the entire antero-ventral surface is traversed by parallel longitudinal fibers; their arrangement is bilaterally symmetrical even though the shaft of the attachment hook is on the right side. In *falcifera* there is a similar symmetrical system of parallel fibers which arise along the entire length of the bilateral piece that supports the hook.

SUMMARY

The astomatous ciliate *Metaradiophrya asymmetrica* n. sp. (Hoplito-phryidae) is found in the middle third of the intestine of the earthworm *Eisenia lönnbergi*. Of 400 worms examined, 60% were infected.

Its structure and method of reproduction by transverse unequal

fission are described and the points in which it differs from *M. lumbrici* and *M. falcifera* are enumerated and discussed.

Neither encystment nor conjugation was observed, and its method of transmission from host to host remains to be ascertained.

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## EXPLANATION OF PLATES 10 AND 11

The writer is indebted to Mrs. Cecil Johnson and Mr. D. D. Ritchie for assistance in the preparation of the figures.

## ABBREVIATIONS

AF, area of right antero-ventral surface that is free of fibers; BG, basal granule; CR, longitudinal ciliary rows; CV, contractile vacuole; D, depression or excavation in antero-ventral surface; DH, developing hook of satellite; EC, ectoplasm; EN, endoplasm; F, supporting fibers of left antero-ventral surface; H, attachment hook; LF, longitudinal fibril connecting the basal granules; MA, macronucleus; MI, micronucleus; P, polygonal area on surface brought out by silver treatment; S, shaft of hook; TF, tuft of supporting fibers on right side at end of shaft.

## PLATE 10

*Metaradiophrya asymmetrica* n. sp.

- Fig. 1. Ventral view of medium-sized individual ( $135\mu \times 55\mu$ ) fixed in Schaudinn's fluid and stained in Mallory's anilin blue-orange G-acid fuchsin. Specimens undergo very little distortion upon fixation in Schaudinn's or Bouin's fluid, so that the normal shape is fairly accurately represented. The figure shows the correct number of ciliary rows and supporting fibers. Camera lucida.  $\times 800$ .
- Fig. 2. Free-hand drawing of medium-sized living individual to show normal shape as viewed from right side. Micronucleus supplied from stained specimens.  $\times 800$ .
- Fig. 3. Free-hand drawing of maximum-sized living individual viewed from right side. To show the thinness of the posterior half and the concavity of the ventral surface in large specimens. Length,  $160\mu$ .  $\times 350$ .
- Fig. 4. Cross section through anterior end of animal at level of supporting fibers. The absence of a peripheral ectoplasmic thickening and the presence of cilia over the entire ventral surface indicate that this region does not function as a sucker.  $\times 800$ .
- Fig. 5. Portion of surface of specimen treated with silver nitrate according to Klein's method to show the surface markings (polygons), basal granules and longitudinal fibrils that connect the granules.  $\times 5000$ .

## PLATE 11

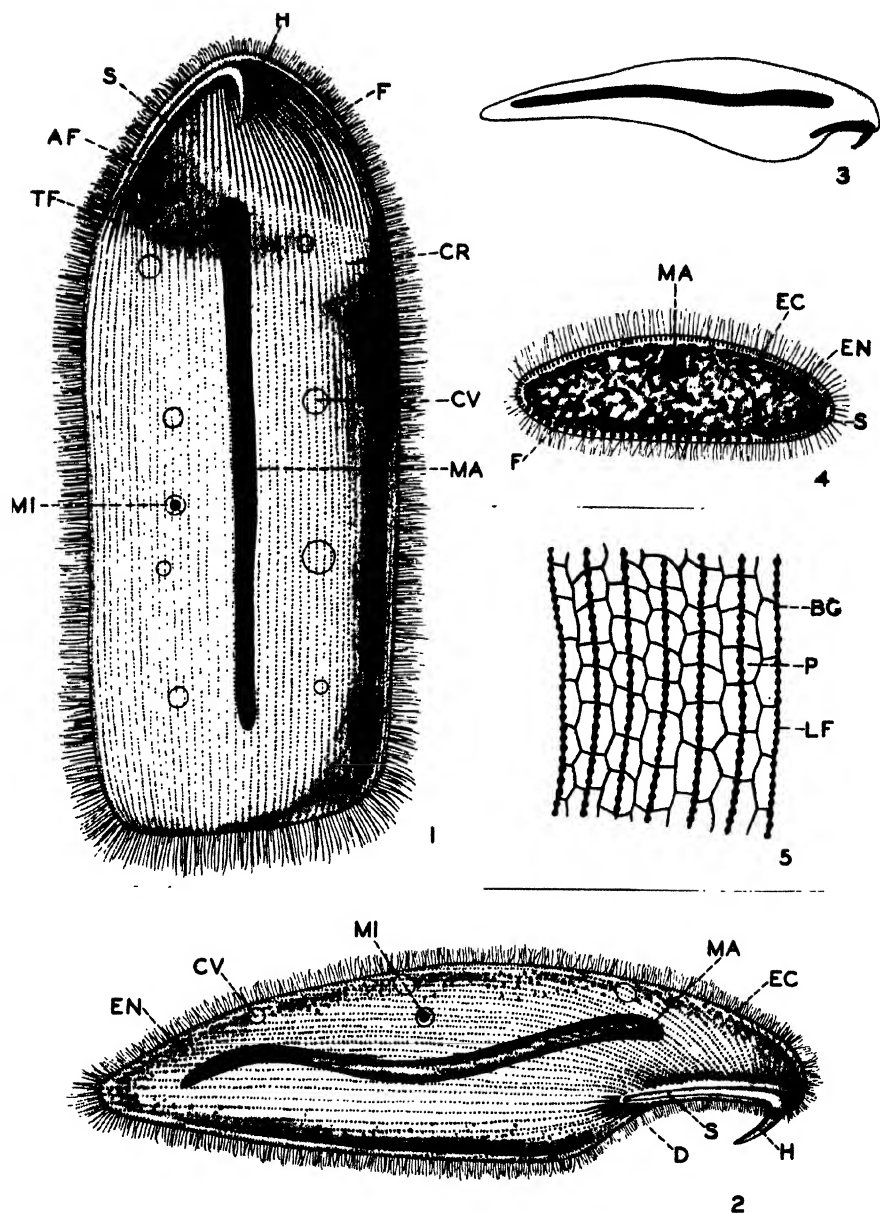
*Metaradiophrya asymmetrica* n. sp.

- Fig. 6. Early division stage; dextro-ventral view. Note that the plane of fission is between the middle and posterior thirds. (In figures 6-11 no attempt has been made to show all of the ciliary rows and supporting fibers.) Camera lucida. Bouin; Delafield's haematoxylin.  $\times 425$ .

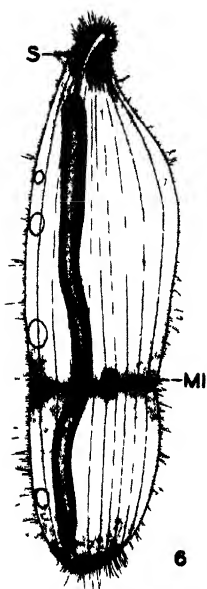
- Fig. 7. Division; ventral view; micronucleus in metaphase. Camera lucida. Bouin; iron haematoxylin.  $\times 425$ .
- Fig. 8. Division; ventral view; micronucleus in anaphase; slight constriction of macronucleus. Camera lucida. Bouin; Delafield's haematoxylin.  $\times 425$ .
- Fig. 9. Division; ventral view; micronucleus in late telophase; division of macronucleus. Camera lucida. Bouin; Delafield's haematoxylin.  $\times 425$ .
- Fig. 10. Division; ventral view; hook developing in the posterior daughter cell (satellite). Camera lucida. Schaudinn; iron haematoxylin.  $\times 425$ .
- Fig. 11. Late division stage; dorsal view; satellite ready to separate from primite. Camera lucida. Schaudinn; Mallory's triple stain.  $\times 425$ .
- Fig. 12. Dividing specimen from right side (stage of fig. 8) to show small size of satellite (left) as compared with primite. Camera lucida; drawn unmounted in Bouin's fluid to eliminate possibility of compression by cover glass.  $\times 350$ .
- Fig. 13. Micronucleus of specimen shown in figure 7; enlarged to show spindle fibers and appearance of chromosomes at metaphase.  $\times 1750$ .
- Fig. 14. Micronucleus of specimen shown in figure 8.  $\times 1750$ .
- Fig. 15. Dividing micronucleus of specimen shown in figure 9. Chromosomes becoming resolved into condition of the resting karyosome; portion of dividing macronucleus alongside.  $\times 1750$ .



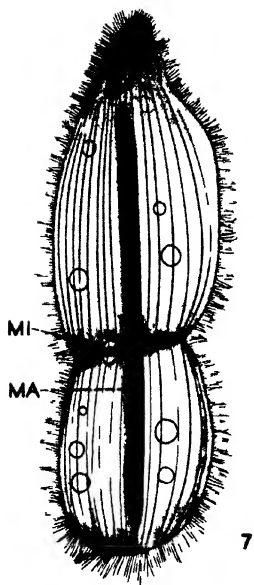
# PLATE 10



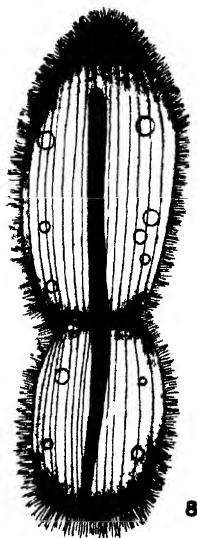




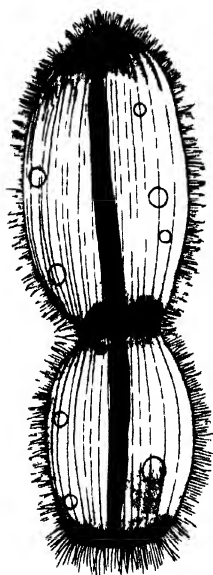
6



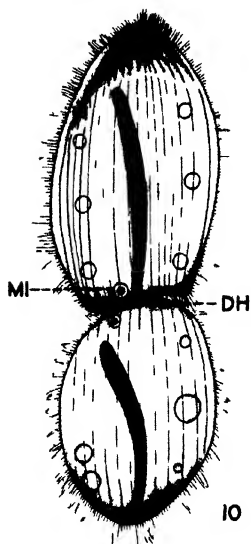
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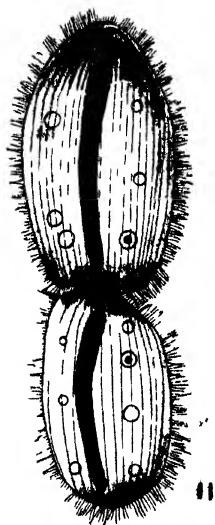
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## MORE PRIMITIVE MOSS-MITES OF NORTH CAROLINA—III

By ARTHUR PAUL JACOT

### PLATES 12 AND 13

The species of Oribatidae here described are Parhypochthoniinae and Hypochthoniinae as delimited in my first paper of this series (4). I find it advisable to segregate in a separate tribe the three genera of Parhypochthoniinae in which the anteriormost transverse row of notogastral bristles comprises eight bristles, namely: the *Palaeacarini* with *Palaeacarus* as type.\* These genera may be separated by means of the following key:

#### KEY TO GENERA OF PALAEACARINI

- |   |                    |
|---|--------------------|
| Dorsum of abdomen crossed by two transverse folds .....       | <i>Aphelacarus</i> |
| Dorsum of abdomen crossed by but one complete transverse fold | <i>Palaeacarus</i> |
| Dorsum of abdomen without transverse folds . . . . .          | <i>Acaronychus</i> |

Figures accompanying this paper represent the animals as seen in balsam mounts, rather than depict details of morphology. Types are to be deposited at the National Museum.

#### *Palaeacarus appalachicus* sp. nov.

##### Figures 1, 2

Differs from *P. araneola* (2, p. 417, figs. 5-7) in having longer, stouter bristles; simple bristlelike pseudostigmatic organs; a normal number of abdominal bristles; more attenuate, mesally curved maxillae (figure 2); and finely ciliate bristles b2, b3, d3, and e1 (the eight largest of the notogaster); unguis with only two (subequal) hooks of which the lateral are a little longer. Size of extended female 0.368 mm., breadth 0.167 mm.

Thus this species is more primitive (except in the modification of the

\* If *Archeonothrus* belongs in this tribe—a point impossible to determine from Trägårdh's very insufficient figures (7)—the name of the tribe will have to be changed to *Archeonothrini*.

maxillae). The anal covers bear but four bristles, the adanals five. The genital covers bear seven bristles which are not quite linearly arranged, in mesal row, and two in lateral row. The aggenital (?) bristles number three. Thus the genital area is the same as in *Acaronychus*. Notogastral bristles d4 are on the rim of the notogaster on the ventral face.

This is the first record of this genus from the United States. The females bear one rather globular egg at a time (possibly two).

This species differs from *P. hystricinus* (7) (the genotype and most closely related described species) of Sweden, in the much shorter cephaloprothorax; much shorter bristles c1; much longer bristles d3; in having one pair less of conspicuous dorsoabdominal bristles; and, possibly, cilia all around the eight major bristles of dorsum of abdomen.

Cotypes: Thirty adults and immatures from litter of seventy year old old-field pine-oak woods, laboratory grounds, Bent Creek Experimental Forest, Buncombe Co., N. Car.; taken September 13th, slide 34F3.2-2.

***Acaronychus trågårdhi longipilus* subsp. nov.**

Differs from the species (2, p. 421, figs. 8-10) in that all of the long bristles are stout, weakly and distantly barbed (except rostrals); upper exopseudostigmatic bristles are strongly bent; dorsoposterior bristles c1 are very long (three times length of other bristles), weakly and distantly barbed; the clavate bristles of posterior end of abdomen (d1) are as long as tibia or genual, longer than either of the two trochanters. The location of the bristles is the same.

Cotypes: Six specimens from pine litter, of uneven-aged old-field, Stadley Hill, six miles south of Asheville, N. Car.; taken October 30th, slide 34F15.23.

One of the outstanding problems in the study of the Oribatidae is the homology of the notogastral bristles. Since the Parhypochthoniinae include the most primitive species they should indicate the primitive condition. The outstanding contribution of the species of *Aphelacarus*, *Palaeacarus*, and *Acaronychus*, that is the tribe *Palaeacarini*, is the presence of eight bristles in the anterior transverse row (row *a*). The fourth or lateralmost bristle (a4) is quite small but quite evident. Unlike other *Parhypochthoniinae*, row *a* is followed (posteriorly) by a transverse fold or suture. One would expect another such fold behind the second transverse row, a condition which apparently is common

to many other Oribatidae, but there is only a partial fold, best developed on the sides. It indicates that the eight bristles of row *b* have already become strongly staggered (figure 1). So much are these bristles displaced that their homology is not clear except by careful comparison of all known species. It then becomes evident that the notogastral bristles are displaced anteroposteriad much more easily than lateromesad. Accepting this as a principle we can designate the anteriormost large ciliate bristle of figure 1 as *b*3 and the next one posteriad as *b*2. Bristles *b*1 are always anteriormost and closest to median plane. The bristles of row *c* of figure 1 are: the minute bristle (*c*2) at foot of the large ciliate bristle (*d*3), the bristle posterolaterad of this pair (*c*4), while the others are obvious. A second *principle* now becomes apparent, namely, alternate bristles of a transverse row tend to migrate together. The minute bristle at foot of the posteriormost large ciliate bristle (*e*1) is *d*1. Bristles *d*4 are on ventral aspect.

***Brachychthonius latus* (5, p. 248)**

In the original description reference to the cotypes was overlooked. The sixty-eight cotypes are from the same sample as the specimens mentioned but are on slide 34F9.2-6.

***Brachychthonius prior* sp. nov.**

Figure 3

Notogastral bristles short, fine, the position of those of anterior transverse plate of dorsum of abdomen as in *B. perpusillus* (5, p. 1, pl. 20, fig. 1) (figure 3); thus resembling *B. bifurcatus* but pseudostigmatic organ head pointed, and the barbs quite distinct, that is, of the usual type; body smooth and puffy, the cephaloprothorax with a small crescent beneath exopseudostigmatic bristles; color pale yellow; size medium (for the genus): length of ovigerous females 0.19 to 0.22 mm. (depending on extension of midthoracic region), breadth 0.096 mm. Thus relatively longer than *B. perpusillus*.

Cotypes: Ninety-one specimens from leaf litter, Robinia stand, Copper Basin, Polk Co., Tenn.; taken November 1st, 1935, by H. J. Loughhead, slide 35FC1-5.

***Brachychthonius attenuatus* sp. nov.**

Figure 9

Bristles short, simple (as *B. bifurcatus*) (5), typically located; no sculpturing; pseudostigmatic organ head dense, nearly smooth, very

maxillae). The anal covers bear but four bristles, the adanals five. The genital covers bear seven bristles which are not quite linearly arranged, in mesal row, and two in lateral row. The aggenital (?) bristles number three. Thus the genital area is the same as in *Acaronychus*. Notogastral bristles d4 are on the rim of the notogaster on the ventral face.

This is the first record of this genus from the United States. The females bear one rather globular egg at a time (possibly two).

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Cotypes: Thirty adults and immatures from litter of seventy year old old-field pine-oak woods, laboratory grounds, Bent Creek Experimental Forest, Buncombe Co., N. Car.; taken September 13th, slide 34F3.2-2.

***Acaronychus trågårdhi longipilus* subsp. nov.**

Differs from the species (2, p. 421, figs. 8-10) in that all of the long bristles are stout, weakly and distantly barbed (except rostrals); upper exopseudostigmatic bristles are strongly bent; dorsoposterior bristles c1 are very long (three times length of other bristles), weakly and distantly barbed; the clavate bristles of posterior end of abdomen (d1) are as long as tibia or genual, longer than either of the two trochanters. The location of the bristles is the same.

Cotypes: Six specimens from pine litter, of uneven-aged old-field, Stadley Hill, six miles south of Asheville, N. Car.; taken October 30th, slide 34F15.23.

One of the outstanding problems in the study of the Oribatidae is the homology of the notogastral bristles. Since the Parhypochthoniinae include the most primitive species they should indicate the primitive condition. The outstanding contribution of the species of *Aphelacarus*, *Palaeacarus*, and *Acaronychus*, that is the tribe *Palaeacarini*, is the presence of eight bristles in the anterior transverse row (row *a*). The fourth or lateralmost bristle (a4) is quite small but quite evident. Unlike other Parhypochthoniinae, row *a* is followed (posteriorly) by a transverse fold or suture. One would expect another such fold behind the second transverse row, a condition which apparently is common

to many other Oribatidae, but there is only a partial fold, best developed on the sides. It indicates that the eight bristles of row *b* have already become strongly staggered (figure 1). So much are these bristles displaced that their homology is not clear except by careful comparison of all known species. It then becomes evident that the notogastral bristles are displaced anteroposteriad much more easily than lateromesad. Accepting this as a principle we can designate the anteriormost large ciliate bristle of figure 1 as *b*3 and the next one posteriad as *b*2. Bristles *b*1 are always anteriormost and closest to median plane. The bristles of row *c* of figure 1 are: the minute bristle (*c*2) at foot of the large ciliate bristle (*d*3), the bristle posterolaterad of this pair (*c*4), while the others are obvious. A second *principle* now becomes apparent, namely, alternate bristles of a transverse row tend to migrate together. The minute bristle at foot of the posteriormost large ciliate bristle (*e*1) is *d*1. Bristles *d*4 are on ventral aspect.

***Brachychthonius latus* (5, p. 248)**

In the original description reference to the cotypes was overlooked. The sixty-eight cotypes are from the same sample as the specimens mentioned but are on slide 34F9.2-6.

***Brachychthonius prior* sp. nov.**

**Figure 3**

Notogastral bristles short, fine, the position of those of anterior transverse plate of dorsum of abdomen as in *B. perpusillus* (5, p. 1, pl. 20, fig. 1) (figure 3); thus resembling *B. bifurcatus* but pseudostigmatic organ head pointed, and the barbs quite distinct, that is, of the usual type; body smooth and puffy, the cephaloprothorax with a small crescent beneath exopseudostigmatic bristles; color pale yellow; size medium (for the genus): length of ovigerous females 0.19 to 0.22 mm. (depending on extension of midthoracic region), breadth 0.096 mm. Thus relatively longer than *B. perpusillus*.

Cotypes: Ninety-one specimens from leaf litter, Robinia stand, Copper Basin, Polk Co., Tenn.; taken November 1st, 1935, by H. J. Loughead, slide 35FC1-5.

***Brachychthonius attenuatus* sp. nov.**

**Figure 9**

Bristles short, simple (as *B. bifurcatus*) (5), typically located; no sculpturing; pseudostigmatic organ head dense, nearly smooth, very

slender (attenuate); nearly colorless; size rather small: length 0.15 to 0.16 mm., breadth 0.09 to 0.1 mm.

Cotypes: Six specimens from oak litter, west slope of ridge above Poplar Cove, Bent Creek Exp. Forest, Buncombe Co., N. Car.; taken July 29th, slide 35F7.2-2.

**BRACHYCHOTHONIUS gen. nov.**

Resembling *Brachychthonius* but with dorsum of abdomen divided into three *longitudinal* areas by two longitudinal ridges which, in dorsal aspect make the posterior end of abdomen appear bituberculate; cephaloprothorax and dorsum of abdomen usually sculptured; contour of cephaloprothorax otherwise indented so as to give it the appearance (in dorsal aspect) of possessing sclerotized ridges which are in reality the surface of the indentations seen on edge; bristles usually short or highly modified; both shoulder bristles on a distinct oval plate (figure 4); notogastral bristles b2 usually on lateral edge of abdomen; posterior segment of abdomen with only six pairs of bristles on dorsal face (the seventh pair is on posterior end below the mesal pair).

Type: *Brachychochthonius jugatus* sp. nov.

***Brachychochthonius jugatus* sp. nov.**

Figures 10, 11

Middle area of cephaloprothorax and dorsum of abdomen sculptured by a series of irregular, often angular, narrow, unequal, elongate ovals, each with a median ridge (figure 10); anterior end of cephaloprothorax indented by coarse scallopings; bristles of notogaster short, those of posterior end quite clavate (figure 10); in lateral aspect edge of rostrum is simply carinate (figure 11), the lamellar bristle area angular but not prominent, the profile rather flat; color practically lacking; size rather small: total length 0.16 mm., breadth 0.08 mm.

***Brachychochthonius laevis* sp. nov.**

Figure 5

Body without sculpturing; longitudinal ridges of dorsum of abdomen with their posterior tubercles present; the indentations of anterior end of cephaloprothorax also present (figure 5); all bristles (except rostral) short, those of posterior end of abdomen clavate. Thus resembling an unsculptured *B. jugatus*. The females bear the usual solitary egg. Color yellowish; size somewhat small: total length of ovigerous females 0.169 mm., greatest breadth 0.083 mm.

Cotypes: Thirteen specimens from leaf litter of Robinia stand, Copper Basin, Polk Co., Tenn.; taken November 1st, 1935, by H. J. Loughhead, slide 35FC1-6.

***Brachychochthonius berlesei erosus* subsp. nov.**

Figures 12-14

Sculpturing of cephaloprothorax similar to that of *B. jugatus* but the anterior end less indented; a single large median indentation gives that area the dorsal aspect of having a single transverse ridge (figure 12); central area of notogaster sculptured with oval depressions resembling corrosion or solution pits (hence the name); notogastral bristles short, those of posterior end barely if at all clavate (figure 14). The sculpturing varies with the individual or the age, for in these genera there is a very gradual transition between the different nymphal and the adult stages. The general tendency is for reduction of sculpturing, especially on cephaloprothorax (compare figures 12 and 14). In lateral aspect, edge of rostrum is bicarinate (figure 13), the lamellar bristle area is more bulby, and the profile more irregular (figure 13); color pale (nearly colorless); size somewhat small, total length 0.174 mm., greatest breadth 0.086 mm.

Cotypes: Thirty-three specimens from Liriodendron litter of a north-east cove, east end of Shut-in-Ridge, Bent Creek Exp. Forest, Buncombe Co., N. Car.; taken October 1st, 1934, slides 34F8-9.

Although this form and *B. jugatus* are found in the same handful of litter, *B. b. erosus* is confined to the upper drier layer (the L-layer), while *B. jugatus* is found in the layer below it (the F-layer) characterized by greater moisture, much more fungus, and leaves more or less fragmented.

*Brachychochthonius berlesei* comb. nov. (8, p. 160, fig. 11; 1, p. 220, pl. 19, fig. 39) differs somewhat in sculpturing and in the shape of the notogastral bristles.

***Brachychochthonius rostratus* comb. nov.**

Figure 15

In lateral aspect the rostrum appears very large, almost as high as the cephaloprothorax and the sides of the latter are more sculptured than in the preceding species (figure 15). The rostral bristles are not distinguishable.



***Brachychochthonius italicus spiciger* comb. nov.**

Although the longitudinal ridges of the dorsum of the abdomen are not as marked in this species as in the preceding, so that the posterior end of the abdomen (as seen in dorsal aspect) is usually smoothly rounded, it belongs in this genus. Emaciated or much dried out specimens show the ridges and posterior tubercles; the short bristles, dorsal sculpturing, and sculpturing of the top of the cephaloprothorax indicate this relationship. The figure of this form in the preceding paper (5, pl. 20, fig. 7) should have notogastral bristles b2 removed to lateral edge of abdomen close to the diagonal line formed by the encroachment of the middle segment.

***Brachychochthonius zelawaiensis* comb. nov.****Figure 6**

Specimens received from Max Sellnick are identical with individuals from the mountains of North Carolina. As Sellnick's figure (6, p. 348, fig. 11) might lead one to regard the top of the cephaloprothorax as similar to that of *Eobrachychthonius*, I include a figure showing the ridges and their enclosures. Besides the six pairs of bristles on the posterior segment of the dorsum of the abdomen, there is a pair at the posterior end, barely visible under the mesal pair, and the usual ventral pair near edge of adanal covers.

This species is easily recognized by the large, clavate-spatulate bristles. In the figure some of the bristles are omitted in order to make the sculpturing more distinct. In my specimens, mounted in balsam, the bristles on the dorsal face of the animal are not discernible. In Sellnick's specimens, mounted in Berlese-Faure medium (a gum arabic base), they are quite distinct, and every line of the sculpturing is so clear and distinct that I am constrained to try again this mounting medium for small colorless or nearly colorless species. Its chief drawback,—excessive reduction in drying, is conspicuous in Sellnick's slide, which is half dried out although ringed with asphaltum. To get clarity of detail however, justifies the use of such a temporary medium—at least for part of ones material.

***Brachychochthonius lydiae* sp. nov.****Figures 7, 8**

Closely resembles *B. zelawaiensis* in form, size, and sculpturing but differs from all described species in the shape of its bristles which are

(as seen in balsam mounts) arborescent. Figure 7 illustrates the appearance of the shoulder bristles a4, while figure 8 shows the pattern of the bristles of the posterior end of the abdomen (dorsal aspect); adanal bristles conspicuous; colorless; size small: total length of body 0.14 to 0.15 mm., breadth 0.06 to 0.07 mm.

Holotype: from litter of laurel slick, north slope of Shut-in-Ridge, Bent Creek Exp. Forest, Buncombe Co., N. Car.; taken May 8th, slide 35F1.3-4. Paratype: from pitch-pine litter of old-field, Stradley Hill, three miles north of Bent Creek Exp. Forest, Buncombe Co., N. Car.; taken October 30th, slide 35F15.2B4.

Named after my wife who has spent many tedious hours sorting and mounting material, in addition to aiding me in a multitude of other ways, directly and indirectly.

### **Brachyochthonius crenulatus sp. nov.**

#### Figure 16

Bristles rather long, simple; b3 in the primitive position; cephaloprothorax with precipitous sides and front,—as indicated by the dark stripe seen in dorsal aspect; sculpturing indistinct in balsam mounts, comprising chiefly scalloped patterns as in figure 16; posterior edge of abdomen crenulate; nearly colorless; size medium: length of body 0.17 mm., breadth 0.1 mm.

Of thousands of specimens of *Brachychthonius* and *Brachyochthonius*, I have but three specimens of this species. Holotype: from dogwood litter of thirty year old old-field, laboratory grounds, Bent Creek Exp. Forest, Buncombe Co., N. Car.; taken September 20th, slide 34F4.3-7.

### **EOHYPOCHTHONIUS gen. nov.**

Hypochthoniinae with one prominent transverse fold across back of abdomen behind second transverse row of (6) bristles; ventral plate undivided, anterior end extending to midthoracic constriction, separated from dorsal plates by a distinct suture or fold of flexible skin except along posterior half where it becomes evanescent half way between bristles c4 (which are the only bristles on its edge) and d4; genital plate transversely divided.

Type: *Hypochthonius gracilis* 5, p. 251, pl. 20, fig. 9.

This genus differs from *Hypochthonius* in that the genital covers are transversely divided, and abut parasterna IV; the aggenital plate (as seen in ventral aspect) ends in a point at sides of genital aperture;

notogastral bristles a2 are well developed. In general it is more closely related to *Eniochthonius* than to *Hypochthonius*. In size of aggenital plates it is more primitive than *Eniochthonius*, for these plates get larger from *Brachychthonius* through *Eniochthonius* to *Hypochthonius*!

#### MIGRATIONS OF NOTOGASTRAL BRISTLES

*Brachychthonius* is supposed to be very primitive because of its "segmentation." Accepting it as such and to make it consistent with the *Palaeacarini*, we will recognize the eight anteriormost bristles as a1 to a4,—a3 having slipped posteriad more than the others (4, pl. 1, figs. 3, 4; 5, pl. 20, figs. 1, 7). The two posterior bristles of the anterior "segment" are b1 and b3 (as in the *Palaeacarini*) and the two bristles of the middle "segment" must be b2 and b4 (as in the *Palaeacarini*). In short this middle segment is, in part at least, a false segment which does not necessarily indicate a primitive condition. If it is a true segmental fold, then *Brachychthonius* is more primitive than the *Palaeacarini*! This notation is corroborated in the figure of the larva of *Sphaerochthonius* (3, p. 24, fig. 2A, 2B) where the four bristles a1 to a4 (called c1 to c3 and d3 by Grandjean) are on the anterior segment; while b1 to b2 (bristles d1, d2, e1, e2 of the figure) are on the next two segments. It is also corroborated by the change in position of bristle a3 in *Eniochthonius* from larva to adult (3, p. 25, fig. 3C to 3A), that is progressively more in line with bristles b1 and b3. Bristles a4 always remaining anchored in their corner.

The posterior segment possesses fourteen bristles on the dorsal face arranged as in *B. perpusillus* (5, pl. 20, fig. 1), and two on the ventral face. The eight anteriormost of these are probably the *c* group, while the other eight are the *d* group with either e1 lost or one of the *d* group lost, who can say which?

In *Brachychthonius* b1 and b3 are fairly close together. In *Eobrachychthonius* and *Brachychochthonius* b3 has migrated to the lateral end of the plate (compare figures 3 and 9 with figures 6, 10, 12, and 14), as had so many of the other bristles. In this respect *Brachychthonius* is more primitive. As to the posterior plate: in *Brachychthonius* c4 is peripheral while d3 is not, while in *Brachychochthonius* c4 is not peripheral while d3 is peripheral (using the term peripheral to designate the sides of the abdomen as viewed in dorsal aspect, which in these two genera is the lateral edge of the dorsal plates). Finally in *Brachychthonius* d2 is laterad of d1, while in *Brachychochthonius* d2 is ventrad of d1.

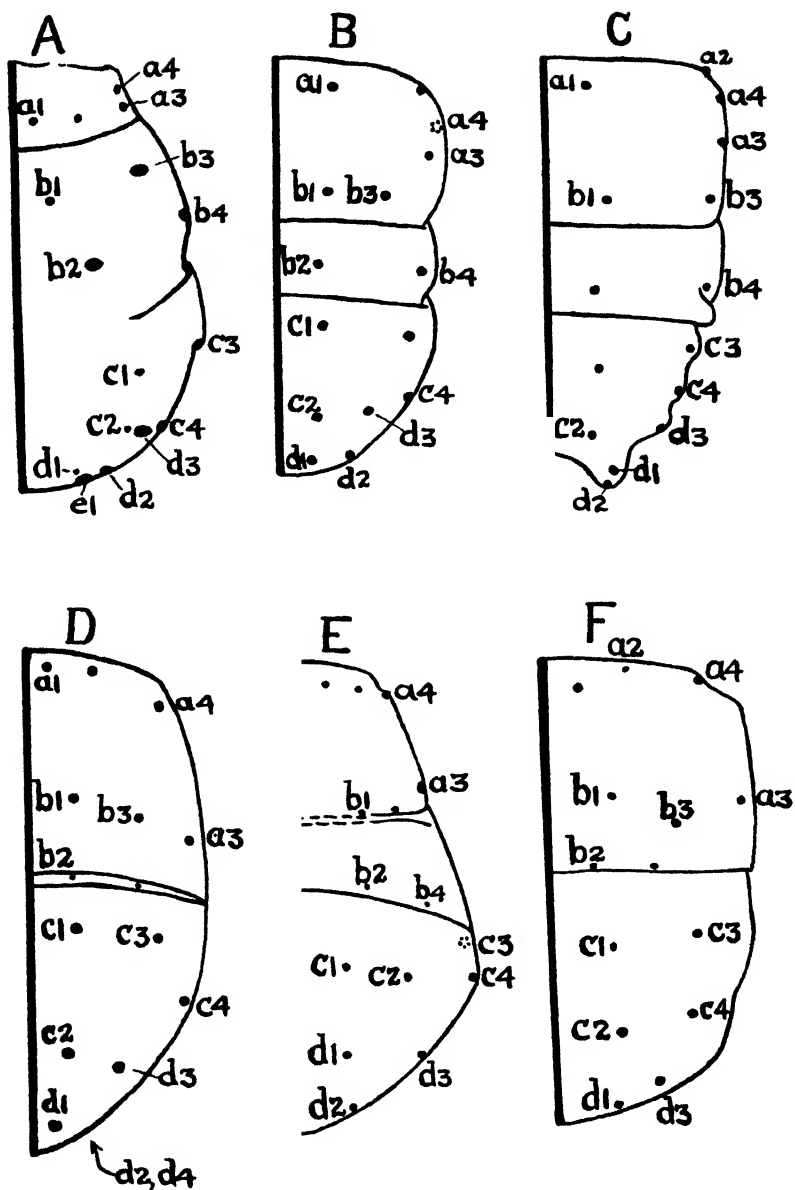


DIAGRAM OF LOCATION OF BRISTLES OF DORSUM OF ABDOMEN

A = Palaeacarus, B = Brachychthonius, C = Brachyochthonius, D = Eohypochthonius, E = Eniochthonius, F = Hypochthonius.

In Eniochthonius, Eohypochthonius, and Hypochthonius, bristles a1 to a4 and b1 to b4 have taken up similar positions, except that a3 has dropped back to be in line with b1 and b3, which must have occurred before b3 became peripheral. As for the posterior segment: Eohypochthonius resembles Brachychthonius except that d2 has become ventral; Eniochthonius is a law unto itself; Hypochthonius appears more primitive in that neither c4 nor d3 have yet become peripheral.

These modifications are graphically presented in the diagram. It is evident from all this that some bristles are more stable than others, and that of the mobile bristles, some move more rapidly than others. To put it more succinctly, a bristle may migrate at different rates in different genera. This law produces radiate in contrast to monolinear evolution.

NORTHEASTERN FOREST EXP. STATION,  
NEW HAVEN, CONN.

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#### PLATE 12

Fig. 1  $\times$  300; all others  $\times$  630.

*Palaeacarus appalachicus* sp. nov.

Fig. 1. Dorsal aspect of abdomen.

Fig. 2. Dorsal aspect of maxillae.

*Brachychthonius prior* sp. nov.

Fig. 3. Dorsal aspect of cephaloprothorax and anterior abdominal segment.

***Brachychochthonius sp.***

Fig. 4. Lateral aspect of anterior and middle abdominal segments, showing bristles a2, a3, b3, b4 (a3 masked by rim of sclerite).

***Brachychochthonius laevis sp. nov.***

Fig. 5. Dorsal aspect of cephaloprothorax.

***Brachychochthonius zelawaiensis comb. nov.***

Fig. 6. Dorsal aspect of cephaloprothorax and anterior abdominal segment, several of the bristles omitted.

***Brachychochthonius lydiae sp. nov.***

Fig. 7. Dorsal aspect of bristle a2 (shoulder bristle).

Fig. 8. Dorsal aspect of bristles of posterior end of abdomen.

***Brachychthonius attenuatus sp. nov.***

Fig. 9. Dorsal aspect, legs and mouth parts omitted.

## PLATE 13

All figures  $\times 630$ .

***Brachychochthonius jugatus sp. nov.***

Fig. 10. Dorsal aspect, legs and mouthparts omitted.

Fig. 11. Lateral aspect of dorsal profile of cephaloprothorax.

***Brachychochthonius berlesel erosus subsp. nov.***

Fig. 12. Dorsal aspect of cephaloprothorax and anterior abdominal segment.

Fig. 13. Lateral aspect of dorsal profile of cephaloprothorax (slightly from above).

Fig. 14. Dorsal aspect of another individual (nymphal?).

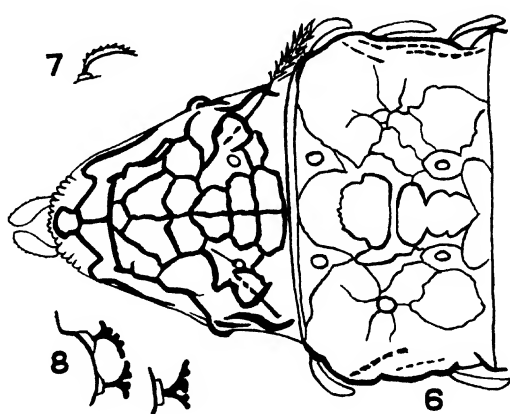
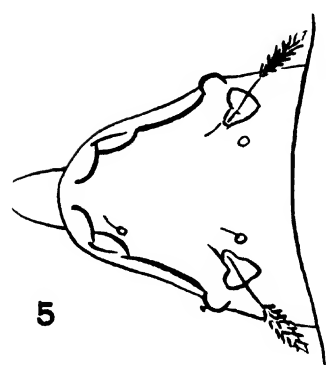
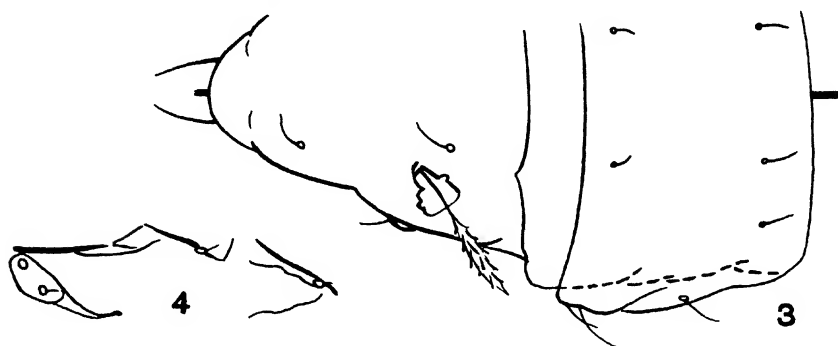
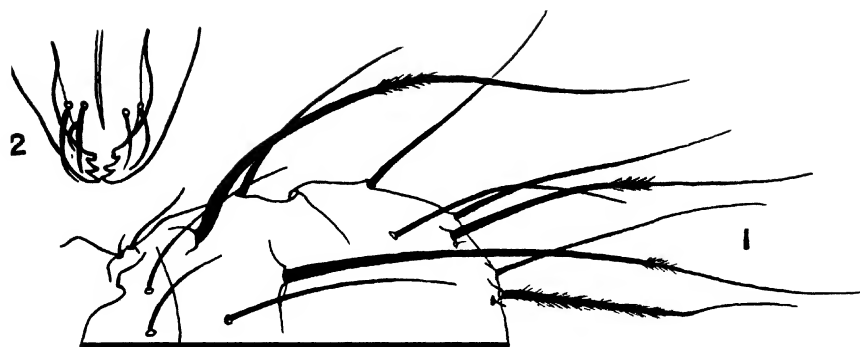
***Brachychochthonius rostratus comb. nov.***

Fig. 15. Lateral aspect of cephalon.

***Brachychochthonius crenulatus sp. nov.***

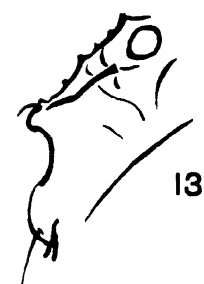
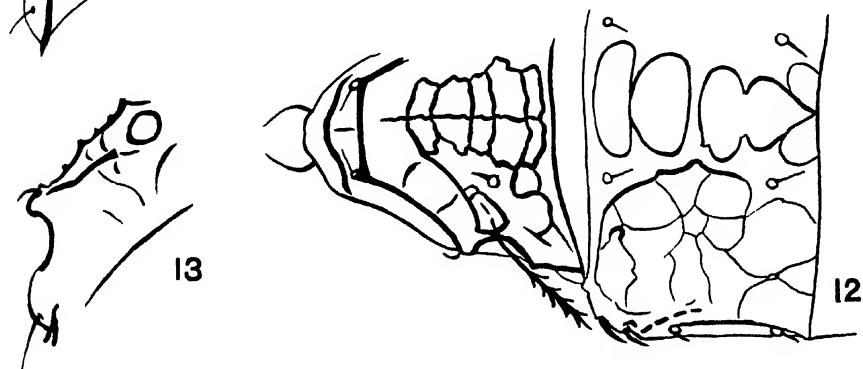
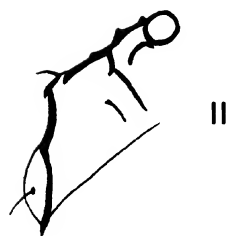
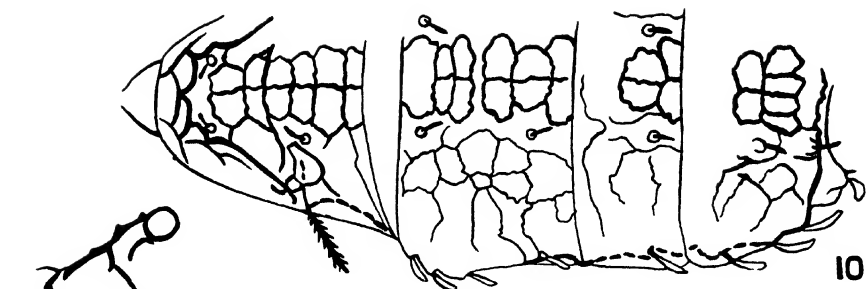
Fig. 16. Dorsal aspect, legs and mouthparts omitted.













## AGARICUS AT GAINESVILLE, FLORIDA

By WILLIAM A. MURRILL

### PLATE 14

Members of the genus *Agaricus* are always interesting because of their use as food. I find the species at Gainesville, Fla., very similar to those recorded by Prof. W. C. Coker for Chapel Hill, N. C., but with exceptions as noted in the following list:

#### ***Agaricus campester* L.**

Common at times, especially in spring and fall, but not nearly so abundant as in the meadows and pastures and old fields of Virginia and other more temperate regions.

#### ***Agaricus comtulus* Fr.**

Common in the woods here, at times appearing in patches containing hundreds of sporophores. The stipe is always rather long and slender.

#### ***Agaricus floridanus* Pk.**

Described from specimens collected by Dr. G. C. Fisher at De Funiak Springs, Florida, in 1910 and collected by me rarely in sandy soil both at Green Cove Springs and at Gainesville. I photographed some of the sporophores, then dried them, and ate the rest.

#### ***Agaricus pratensis* Scop.**

A fine edible species, but unfortunately rare here. Most of my friends prefer it under another name.

#### ***Agaricus sylvicola* (Vitt.) Sacc.**

A beautiful white species occurring commonly in our woods. Peck's name, *A. abruptibulbus*, is more descriptive, unless Vittadini had in mind some fair sylvan nymph.

#### ***Agaricus placomyces* Pk.**

Common in woods here, just as I remember it in New York and Virginia. As Coker remarks, the specimens fit the pictures.

**Agaricus auricolor** Krieger

Known to the older mycophagists as Curtis' almond mushroom, but he failed to describe it. I have seen it and enjoyed it here for several years. Last summer it appeared abundantly on a shaded lawn where manure mixed with sawdust had been scattered. The young sporophores are often exactly cylindric. Dried specimens are yellow like those of the horse mushroom, thus meriting the name assigned by Krieger. A full and illustrated account of this interesting species was given by Dr. W. C. Coker in his article on *Psalliota* in this Journal, vol. 43: 249, 1928.

**Agaricus diminutivus** Pk.

A small form of this species with slender stipe grows sparingly in mixed oak and pine woods here, appearing in patches of a dozen or more sporophores. In shape it resembles *A. comtulus* Fr., but the cap is a pretty reddish-pink when fresh, becoming reddish-brown when dried. There is also a slight umbo at times and the fibrillose scales are always present as described by Peck.

**Agaricusalachuanus** sp. nov.

Pileus convex to slightly depressed, gregarious, about 3-4 cm. broad; surface dry, isabelline, with purple scales arranged in an imbricate pattern as in *A. placomyces*, not becoming darker on drying, purplish-brown on the disk; context white; lamellae as usual for the genus, almost black with age; spores subellipsoid, smooth, dark-brown,  $6 \times 3.5\mu$ ; stipe white, smooth, rather thick, bulbous, not exceeding 4 cm. in length; annulus ample, persistent, white, becoming yellow on drying.

Type collected by W. A. Murrill in a low spot under a laurel oak in Gainesville, Fla., August 17, 1937 (No. 15917). From our other small species, *A. comtulus* and *A. diminutivus*, this one differs decidedly in its shorter, thicker stipe and conspicuous purple scales. From small forms of *A. micromegethus*, the ample, persistent annulus would at once distinguish it. Some of my readers might like to know that Gainesville is situated in Alachua County, an Indian word more difficult to pronounce properly than to spell correctly.

**Agaricus praemagniceps** sp. nov.

Pileus cylindric-truncate to convex, expanding and finally depressed, gregarious, reaching fully 15 cm. in diameter; surface uniformly rosy-avellaneous when young, becoming pallid at maturity with the disk

sprinkled over with minute avellaneous fibrils; context white, scarcely changing, of good flavor but too tough and stringy for enjoyment; lamellae white when young, almost black with age; spores ovoid, smooth, dark-brown,  $6 \times 3.5-4\mu$ ; stipe very white, smooth, glabrous, nearly equal, abruptly bulbous, about  $6-10 \times 1-1.5$  cm.; annulus white, single, ample, persistent.

Type collected by W. A. Murrill under a laurel oak in Gainesville, Fla., August 15, 1937 (No. 16051). Also collected by the author several other times under evergreen oaks about Gainesville in late summer or early fall. In view of its size and attractive appearance, it was quite disappointing to find it rather an exception for the genus from the standpoint of the mycophagist.

#### NEW COMBINATIONS

For those using a different nomenclature the following transfers are made:

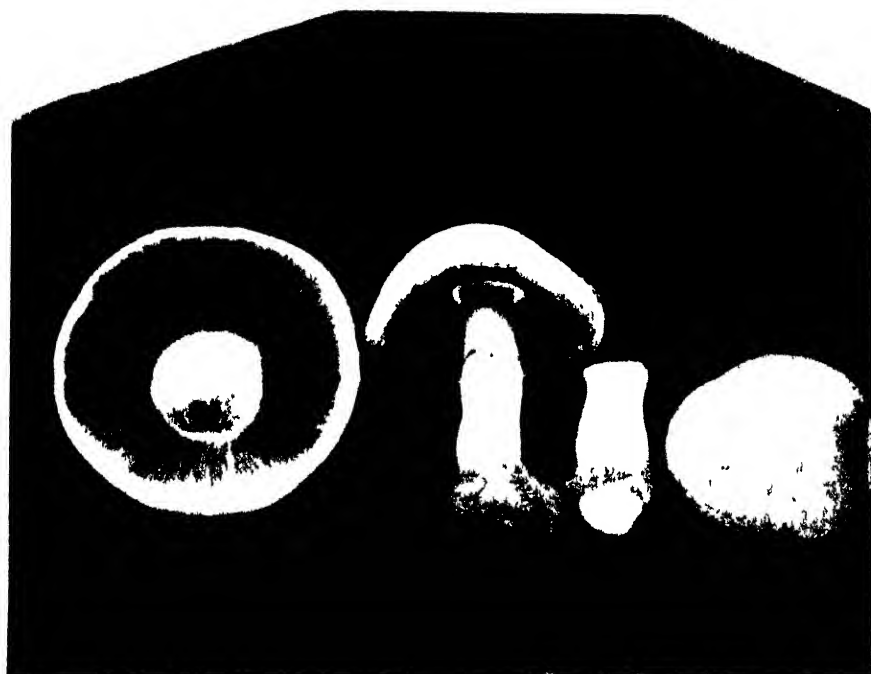
*Agaricus alachuanus* = *Psalliota alachuana*.

*Agaricus praemagniceps* = *Psalliota praemagniceps*.

GAINESVILLE, FLA.



PLATE 14



AGARICUS FLORIDANUS PK X  $\frac{1}{2}$   
(Photograph by the author)





# ATMOSPHERIC POLLEN SURVEY OF CHARLOTTESVILLE, VIRGINIA, FOR 1936<sup>1</sup>

By ELTON C. COCKE

It is a well established fact that all true hayfever is caused by pollen. This pollen may be inhaled from the normal pollen content of the air as the victim goes about his daily duties, or it may be gotten by direct contact with flowers; the latter cases occur chiefly among gardeners and punctilious housewives who carefully arrange daisies and daffodils, goldenrods and chrysanthemums in vases about the house. By far the greater majority of cases of hayfever are caused by wind-blown pollen which invades the atmosphere from early spring to late fall. It is obvious that an accurately determined pollen survey furnishes the best clue to the hayfever potentialities of any given locality. The pollen cycle is repeated year after year with only slight variations due to seasonal conditions. Every community should, therefore, have a reliable pollen survey made and the data obtained recorded in readily available form. It is the purpose of this paper to record and discuss the pollen content of the air at Charlottesville, Virginia, during 1936, as determined by results obtained from the examination of slides exposed daily during the entire year.

Charlottesville is located in Albemarle County near the geographical center of Virginia in the foothills of the Blue Ridge Mountains. The elevation is about 500 feet above sea level. The city is more or less surrounded by low mountains which are covered by a mixed hardwood type of forest, with oak predominating. Approximately 41% of the land of Albemarle County is either in cultivation or in open pasture. Patches of scrub pine are to be found in many abandoned fields nearby.

Neff (1) listed the trees given in Table I as native to Albemarle. Their relative abundance is also given. In addition to the native species there are many exotic trees planted on the University of Virginia grounds. Paper mulberry which is common as an escape, cypress, and spruce are the only introduced genera which shed enough pollen into the atmosphere to be important in a pollen survey.

<sup>1</sup> Contribution from Miller School of Biology, University of Virginia.

TABLE I  
Native Trees of Albemarle

COMMON NAME	BOTANICAL NAME	RELATIVE ABUNDANCE
Alder	<i>Alnus serrulata</i>	Abundant along streams
Ash, white	<i>Frazinus americana</i>	Common
Ash, red	<i>F pennsylvanica</i>	Common along streams
Aspen, large tooth	<i>Populus grandidentata</i>	Rare
Basswood	<i>Tilia americana</i>	Common
Beech	<i>Fagus grandifolia</i>	Common
Birch, black	<i>Betula lenta</i>	Common along streams
Birch, yellow	<i>B lulea</i>	Common along streams
Boxelder	<i>Acer Negundo</i>	Scarce
Buckeye	<i>Aesculus glabra</i>	Rare
Cedar, red	<i>Juniperus virginiana</i>	Abundant
Cherry, wild	<i>Prunus serotina</i>	
Chestnut	<i>Castanea dentata</i>	Mostly killed out
Chinquapin	<i>C pumila</i>	Common
Cottonwood	<i>Populus alba</i>	Rare
Cucumber tree	<i>Magnolia acuminata</i>	Rare
Dogwood	<i>Cornus florida</i>	Abundant
Elm, American	<i>Ulmus americana</i>	Common
Gum, black	<i>Nyssa sylvatica</i>	Common
Hackberry	<i>Celtis occidentalis</i>	Scarce
Hickory, mockernut	<i>Carya alba</i>	Abundant
Hickory, shellbark	<i>C ovata</i>	Rare
Hickory, pignut	<i>C glabra</i>	Common
Hickory, bitternut	<i>C cordiformis</i>	Rare
Hornbeam	<i>Ostrya virginiana</i>	Common along streams
Holly	<i>Ilex opaca</i>	Common
Ironwood	<i>Carpinus caroliniana</i>	Common along streams
Locust, black	<i>Robinia pseudo-acacia</i>	Abundant
Locust, honey	<i>Gleditsia triacanthus</i>	Common
Maple, black	<i>Acer nigra</i>	Rare
Maple, silver	<i>A saccharinum</i>	Common
Maple, red	<i>A rubrum</i>	Abundant
Mulberry, red	<i>Morus rubra</i>	Common
Oak, white	<i>Quercus alba</i>	Abundant
Oak, red	<i>Q rubra</i>	Abundant
Oak, post	<i>Q stellata</i>	Abundant
Oak, chestnut	<i>Q prinus</i>	Common
Oak, black	<i>Q velutina</i>	Abundant
Oak, scarlet	<i>Q. coccinea</i>	Abundant
Oak, Black Jack	<i>Q marilandica</i>	Common
Oak, Spanish	<i>Q falcata</i>	Abundant
Oak, pin	<i>Q palustris</i>	Common
Osage orange	<i>Maclura pomifera</i>	Common
Pawpaw	<i>Asimina acuminata</i>	Rare

TABLE I—*Concluded*

COMMON NAME	BOTANICAL NAME	RELATIVE ABUNDANCE
Paulownia	<i>Paulownia tomentosa</i>	Rare
Persimmon	<i>Diospyros virginiana</i>	Scarce
Plum, wild	<i>Prunus nigra</i>	Scarce
Pine, white	<i>Pinus strobus</i>	Abundant
Pine, Jersey	<i>P. virginiana</i>	Abundant
Pine, pitch	<i>P. rigida</i>	Common
Pine, yellow	<i>P. echinata</i>	Abundant
Redbud	<i>Cercis canadensis</i>	Abundant
Sassafras	<i>Sassafras variifolium</i>	Abundant
Service berry	<i>Amelanchier canadensis</i>	Common
Sycamore	<i>Platanus occidentalis</i>	Common
Walnut, black	<i>Juglans nigra</i>	Common
Walnut, white	<i>J. cinerea</i>	Common
Willow, black	<i>Salix nigra</i>	Common along streams

The common grasses and wind pollinated weeds of this vicinity are listed in Table II. Several species of golden rod are abundant, but since these are not generally wind pollinated they do not contribute appreciably to the atmospheric pollen.

#### METHODS

Microscopic slides coated with Brandt's glycerine jelly to which methylene green had been added were exposed to the atmosphere for 24 hours. At the end of the exposure period the slides were taken into the laboratory, warmed gently to drive off excess moisture, then a drop of warm glycerine jelly added and a #1 cover glass put on. The slides were exposed approximately 20 feet from the ground and were protected from sun and rain by a shelter open on two sides.

The slides were examined, all grains carefully identified, and number of each type of pollen recorded for each day. From the number of grains caught per square centimeter the pollen concentration per cubic yard was determined from formula and table given by Cocke (3) based on his revision of Scheppegrell's (4) formula. Due allowance was made for difference in size as well as wings, spines, etc., in determining the number of pollen per cubic yard.

#### RESULTS

Chart I and Table III give the results of the pollen concentration in number of grains per cubic yard from March 1st through October. Even though pollen was caught almost every clear day during the year,

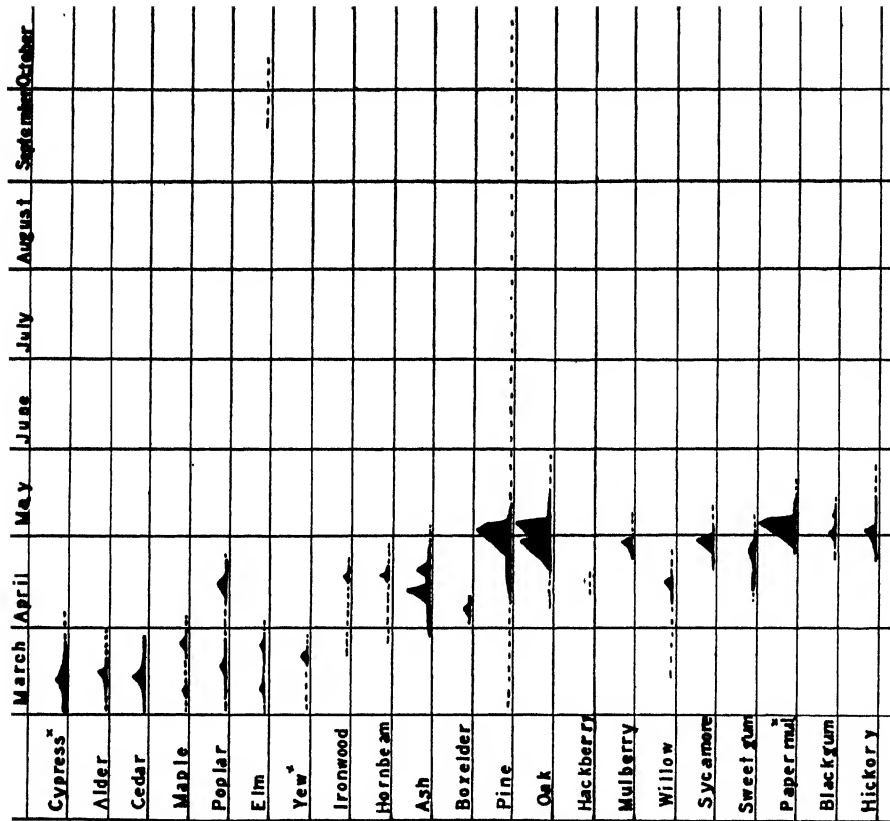
TABLE II





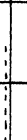









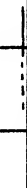



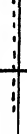


*Common grasses and wind pollinated weeds of Albemarle County*

COMMON NAME	BOTANICAL NAME	BLOOMING DATE
<i>Grasses</i>		
Barnyard grass.....	<i>Echinochloa crus-galli</i>	July-September
Bent grass.....	<i>Agrostis alba</i>	June-July
Blue grass.....	<i>Poa pratensis</i>	June
Broom sedge.....	<i>Andropogon</i>	July-August
Crab grass.....	<i>Digitaria sanguinalis</i>	July-September
Cheat.....	<i>Bromus secalinus</i>	June-July
Darnel.....	<i>Lolium temulentum</i>	June-July
Fescue.....	<i>Festuca</i>	June-July
Foxtail.....	<i>Setaria glauca</i>	July-August
Goose grass.....	<i>Eleusine indica</i>	June-September
Johnson grass.....	<i>Sorghum halepense</i>	June-July
Oat grass.....	<i>Danthonia spicata</i>	June
Orchard grass.....	<i>Dactylis glomerata</i>	June
Poverty grass.....	<i>Aristida dichotoma</i>	August-September
Panic grass.....	<i>Panicum</i>	July-August
Rye grass.....	<i>Lolium perenne</i>	June-July
Sweet vernal.....	<i>Anthoxanthum odoratum</i>	May-June
Timothy.....	<i>Phleum pratense</i>	June
Tall red top.....	<i>Tridens flavus</i>	August-September
<i>Weeds</i>		
Burdock.....	<i>Arctium Lappa</i>	August-October
Cocklebur.....	<i>Xanthium</i>	August-September
Dock, broad leaf.....	<i>Rumex obtusifolius</i>	July-August
Dock, narrow leaf.....	<i>R. crispus</i>	July-September
Goose foot.....	<i>Chenopodium glaucum</i>	August-September
Wormseed.....	<i>C. ambrosioides</i>	August-September
Nettle.....	<i>Urtica</i>	July-September
Lamb's quarters.....	<i>Chenopodium album</i>	August-September
Pigweed, red root.....	<i>Amaranthus retroflexus</i>	August-September
Plantain, broad leaf.....	<i>Plantago major</i>	May-September
Plantain, narrow leaf.....	<i>P. lanceolata</i>	April-September
Ragweed, dwarf.....	<i>Ambrosia artemisiifolia</i>	August-October
Ragweed, giant.....	<i>A. trifida</i>	August-October
Sheep sorrel.....	<i>Rumex acetosella</i>	May-July
Spiny amaranth.....	<i>Amaranthus spinosus</i>	August-September
Tumble weed.....	<i>A. graecizans</i>	July-September
Wormwood.....	<i>Artemisia</i>	August-September

TABLE III

COMMON NAME	BOTANICAL NAME	DATE OF POLLENATION	DATE OF MAXIMUM CONCENTRATION PER CU. YD.	MAXIMUM CONCEN. PER CU. YD.	REMARKS
Maple.....	<i>Acer</i>	Mar. 1-Apr. 3	Mar. 14- Mar. 24	122	Some pollen of these genera was caught as early as Jan. 18
Alder.....	<i>Alnus</i>	Mar. 3-Mar. 30	Mar. 14	135	
Red Cedar.....	<i>Juniperus virginiana</i>	Feb. 28-Mar. 23	Mar. 14	215	
Cypress.....	<i>Taxodium distichum</i>	Mar. 3-Apr. 4	Mar. 14	360	Cypress is rare, but there are several trees nearby
Poplar.....	<i>Populus</i>	Mar. 3-Apr. 20	Mar. 18 Apr. 15	70 130	Two species
Elm.....	<i>Ulmus</i>	Mar. 3-Apr. 4	Mar. 9 Mar. 14	60 66	Pollen of a fall species was caught during Sept. and Oct.
Yew.....	<i>Taxus</i>	Mar. 9-Mar. 25	Mar. 18	40	Cultivated
Ironwood.....	<i>Carpinus</i>	Mar. 25-Apr. 24	Apr. 20	16	Ash is abundant nearby
Hornbeam.....	<i>Ostrya</i>	Mar. 28-Apr. 26	Apr. 20	20	
Ash.....	<i>Fraxinus</i>	Mar. 28-May 2	Apr. 11	700	
Boxelder.....	<i>Acer Negundo</i>	Apr. 4-Apr. 10	Apr. 8	36	Some pine pollen was caught throughout the year
Pine.....	<i>Pinus</i>	Apr. 10-May 10	May 2	960	
Oak.....	<i>Quercus</i>	Apr. 12-May 30	Apr. 28 May 4	814 994	
Hackberry.....	<i>Celtis</i>	Apr. 10-Apr. 14	Apr. 9	6	Rare
Willow.....	<i>Salix</i>	Mar. 14-Apr. 20	Apr. 14	116	Rare
Sweet gum.....	<i>Liquidambar</i>	Apr. 12-Apr. 30	Apr. 25	65	
Hasel.....	<i>Corylus</i>	Mar. 2-Mar. 30	Mar. 14	7	
Mulberry.....	<i>Morus</i>	Apr. 24-May 6	Apr. 26	120	Cultivated
Birch.....	<i>Betula</i>	Apr. 10-May 15	Apr. 14 Apr. 26 May 12	40 40 210	
Sycamore.....	<i>Platanus</i>	Apr. 20-May 4	Apr. 27	210	
Paper mulberry.....	<i>Broussonetia</i>	Apr. 25-May 15	May 4	1020	Common as an escape
Black gum.....	<i>Nyssa</i>	Apr. 25-May 9	May 1	50	
Hickory.....	<i>Carya</i>	Apr. 26-May 15	May 2	180	
Walnut.....	<i>Juglans</i>	Apr. 26-May 31	May 2	66	Cultivated
Spruce.....	<i>Picea</i>	Apr. 25-May 5	May 1	70	
Beech.....	<i>Fagus</i>	Apr. 25-May 10	May 2	9	
Plantain.....	<i>Plantago</i>	May 10-Sept. 8	June 14	38	Only occasional grains
Osgae orange.....	<i>Maclura</i>	May 10-May 16	May 13	216	
Sedges.....	<i>Cyperaceae</i>	Apr. 10-May 15			
Dock.....	<i>Rumex</i>	Apr. 20-May 31	May 4	58	Common nearby
Tree-of-Heaven.....	<i>Ailanthus</i>	May 28-June 25	June 14	70	
Linden.....	<i>Tilia</i>	June 20-July 8	June 29	5	
Locust.....	<i>Gleditsia</i>	May 10-May 27	May 13	40	Cultivated
Grass.....	<i>Gramineae</i>	Apr. 15-Oct. 15	May 8 May 26 June 20 July 10 Sept. 25	60	
Privet.....	<i>Ligustrum</i>	June 14-July 5	June 25	5	
Rushes.....	<i>Juncus</i>	May 10-May 24	May 3	2	Cultivated
Ginkgo.....	<i>Ginkgo</i>	Apr. 29-May 5	May 2	5	
Chenopods.....	<i>Chenopodium</i>	July 26-Sept. 3	Aug. 27	10	
Amaranth.....	<i>Amaranthus</i>	July 12-Sept. 10	Aug. 28	6	Cultivated
Wormwood.....	<i>Artemisia</i>	Aug. 20-Sept. 18	Sept. 5	5	
Flabane.....	<i>Eriogon</i>	Aug. 12-Sept. 14	Sept. 4	4	
Ragweed.....	<i>Ambrosia</i>	Aug. 12-Oct. 30	Aug. 22 Sept. 5	860 1020	Cultivated
Parthenium.....	<i>Parthenium</i>	July 28-Aug. 7	Aug. 4	2	
Goldenrod.....	<i>Solidago</i>	Sept. 10-Oct. 8	Sept. 29	14	
Composites.....	<i>Compositae</i>	Aug. 15-Oct. 10	Sept. 29	5	Cultivated
Cocklebur.....	<i>Xanthium</i>	Sept. 1-Sept. 28	Sept. 16	25	



Birch	
Osage ora	
Plantain	
Dock	
Sedges	
Tree-of-Hes	
Linden	
Hazel	
Locust	
Wormwood	
Parthenium	
Cocklebur	
Golden rod	
Chenopods	
Amaranthus	
Fleabane	
Privet	
Grass	
Ragweed	
Composites	
Rushes	



the grains recorded during November, December, January, and February were mostly relics of the previous season left in the dust, and were not sufficiently abundant to be reckoned with.

Although pollen of early blooming trees occurred spasmodically during warm spells in February, it was not present in sufficient concentration to be important until March 3. On this date cypress, poplar, elm, alder, hazel, cedar, and maple were recorded. These genera constitute the principal flora for March, most of them reaching their peak about the middle of the month. Cypress is not endemic to this area. The high pollen concentration of this genus is due to the presence of several large trees planted close by. Later in March ironwood, hornbeam, willow, and pine begin to occur irregularly. The pine caught during March appears to be fresh, and very probably blew in from farther south, as pines did not begin pollinating at Charlottesville until April 12. The first peak in the poplar curve is due to aspen (*Populus grandidentata*), the second, occurring April 15, represents cottonwood (*Populus alba*).

Cottonwood, ironwood, hornbeam, ash, boxelder, hackberry, mulberry, willow, sycamore, and sweet gum reach their height of pollination during April, as shown by Chart 1. Oak, pine, paper mulberry, hickory, walnut, spruce, black gum, and dock begin to shed their pollen late in April. These genera, however, do not reach their maxima until the first week in May. The two-pointed curve of oak is occasioned by different species, the same is probably true for the three-pointed curve of birch. Osage orange is important about May 15.

There is a decided drop in the pollen concentration of the air during June and July. Only three woody forms, linden, tree-of-heaven, and privet, contribute enough pollen to be recorded on the pollen slides during this period. Plantain and grass, although never contributing large quantities of pollen, do constitute an important part of the pollen flora from the first of May through September. The low concentration of grass pollen is not indicative of a scarcity of grasses, for they are abundant, but is caused by the lowness of the plants and the relatively large size of the pollen grains. The numerous peaks in the grass curve are obviously caused by different blooming dates of various species.

On August 12, seventeen ragweed pollen grains were caught on a single slide. This was sufficient number to indicate that ragweed was actually blooming in the neighborhood. These seventeen grains were identified as giant ragweed (*A. trifida*). The concentration of ragweed

pollen increased rapidly to August 22, when it reached 860 grains per cubic yard. After this date there was a decrease of pollen until September 2, then it began to rise and finally reached the maximum of 1020 grains per cubic yard on September 5. This peak was followed by a sharp decline to 220 grains per cubic yard on September 12, then the count remained more or less constant until September 25. A gradual diminution of ragweed continued until late October, when concentration became so low that it was evident that the ragweed season was over.

Wormwood, golden rod, chenopods, amaranths, fleabane, and unidentified composites are recorded in the chart and Table III. Their concentration never reaches magnitudes sufficient to be considered important, however.

#### DISCUSSION

The old question of "what pollen concentration of the air is necessary to excite hayfever symptoms in sensitive individuals" remains unsettled. Blackley (5) in 1873 concluded that 25 pollen granules inhaled per day were sufficient to cause hayfever. Durham (6) states: "Some ragweed-sensitive persons begin to sneeze by the time the first pollen grains appear in the air. Others do not begin until the air contains ten, twenty, or fifty pollen grains per cubic yard. The inhalation of twenty-five granules of pollen in a day's time is usually sufficient to cause trouble. This is a very small amount when it is remembered that there are billions of ragweed pollen grains in an ounce of pollen. Positive skin tests have been obtained by injecting into the skin the extract of one-tenth of a granule of ragweed pollen" (pp. 132, 133). He does not state here how he arrived at the pollen concentration, though earlier in his book he says that he used Scheppegegrell's formula  $n = 1.8N$ . Since this formula has been proved to be incorrect (Cocke, 2), his estimate of the pollen concentration necessary to excite symptoms may be too low. The same may be true for the estimate given by Feinberg and Steinberg (7) of 25 grains per cubic yard.

Brown (8) is of the opinion ~~that~~ unless pollen applied to the nasal mucous membrane is much more active in producing symptoms than the same amount injected subcutaneously, or ~~else~~ that pollen inhaled from the air has a cumulative effect on the system, the atmospheric pollen concentration necessary to cause hayfever is generally greatly underestimated. Brown makes the following statement:

"Durham (6) has estimated that if a patient were out of doors standing by the pollen slide during the whole twenty-four hours, the maximum

amount he would inhale on the worst day we have had in Washington would be about 4,000 granules. This is allowing 20 cubic yards of air for the twenty-four-hour intake, and multiplying this by the average number of pollen granules per cubic yard of air for the period. This total of 4,000 granules inhaled would represent 8 pollen units, so that the maximum contact in Washington would be only 8 units per day.

"Patients who have worked up to doses of 50,000 or more pollen units, and are taking increases of 5,000 to 10,000 units at a time, certainly would not be affected by an increment of only 8 units. Furthermore, it is the exceptional patient indeed who has any symptoms from a dose of 8 pollen units injected out of season.

"I can think of only three possible explanations for this marked discrepancy. The first and most likely one would be that the estimates as to the amount of pollen inhaled from the air are grossly erroneous. The second explanation would be that 8 units of pollen applied to the nasal mucous membrane is much worse than 8 pollen units injected subcutaneously. The final explanation would be that the pollen inhaled from the air has a cumulative effect in the system."

I have already shown in two previous papers (Cocke, 2, 3) that Brown's first assumption explaining this discrepancy is correct, that is, earlier methods of estimating the pollen concentration per cubic yard have been grossly erroneous. However, the method used in this paper for determining the pollen concentration of the air has been proved both by theory and actual experiment to be approximately correct. But even with the greater concentration of pollen per cubic yard which the present method gives over Scheppegegrell's formula ( $n = 1.8N$ ), there is still a discrepancy existing between the amount of pollen which produces ill effects when breathed as compared with the subcutaneous dose which gives a positive reaction. This fact can be explained, I think, only by Brown's last two assumptions—that is, first, pollen is much more toxic when inhaled than when injected subcutaneously, and, second, pollen inhaled from the atmosphere has a cumulative effect on the system which produces serious effect even when inhaled in minute quantities.

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## OBSERVATIONS ON THE DEVELOPMENT OF A NEW SPECIES OF PHYTOPHTHORA\*

By LELAND SHANOR

PLATES 15 AND 16

While examining for aquatic Phycomycetes some water collections made in high altitude pools in the vicinity of Highlands, N. C., a species of *Phytophthora* growing on the petals of *Rhododendron maximum* which had fallen into a small spring stream was isolated. The spiny nature of the oogonia of this plant immediately attracted the attention of the author as he could not recall having seen any literature on or figures of a species with oogonia of this character. Jones *et al* (1912) had figured resting bodies of *P. infestans* which resemble the oogonia of the present fungus only in their spiny character. The resting bodies figured and described by these authors lacked antheridia and are considered a type of chlamydospore. They could not be considered organs of sexual reproduction.

Wilson, in 1914, reviewed the then known species of *Phytophthora*, basing his taxonomy upon morphological characters and hosts. Rosenbaum (1917) attempted to set up a criterion for species in this genus, using a biometrical scheme based upon spore and sporangial measurements. Leonian (1925, 1934) and Leonian and Geer (1929) have worked out a classification of *Phytophthora* based chiefly upon a physiological separation of species—species that morphologically are often very similar. Leonian and Geer place no confidence in a morphological method of separating species because the size of the sporangia of different strains of the same species often present great variation under uncontrolled cultural conditions. As cultural conditions and hosts are altered (Leonian, 1927), so are the sizes of sporangia. Tucker (1931),

\* This plant was found while the writer was working on a research scholarship granted by the University of North Carolina to study at the Samuel T. Weyman Laboratory, Highlands, N. C., and the investigation was completed in the Botanical Laboratory of the University of North Carolina. He is grateful to Dr. W. C. Coker and Dr. J. N. Couch for helpful suggestions and constructive criticism.

after a careful study of the genus, gives a key for separation and identification of 19 species and one variety. In a later publication (1933) he has compiled a comprehensive bibliography relating to the distribution of the genus. Leonian (1934), after further studies on *Phytophthora*, believes that the genus contains only three good species, namely, *Phytophthora cactorum*, *P. infestans*, and *P. palmivora*. He has, however, given a key whereby 22 species and varieties can be identified.

So far as I have been able to determine there are no known species of *Phytophthora* that have spiny oogonia, and this species is therefore distinct from all others in possessing this characteristic. Since this species has very sharp, gradually tapering spines, the author has selected the name *Phytophthora stellata* as appropriate. The description follows:

***Phytophthora stellata* n. sp.**

Growth delicate on *Rhododendron* petals and on hemp seed in water, quite dense and often reaching out to a length of 1-2 cm. or more. Threads of the mycelium  $3.5-7.0\mu$  thick, mostly about  $5.6\mu$ , very rarely septate; septa, when present, found near reproductive branches or in old cultures. Walls giving a cellulose reaction with chloroiodide of zinc. Sporangia borne either terminally or on short lateral branches, usually somewhat obpyriform, sometimes more oval or more elongated; if terminal measuring from  $80.6-115.8\mu$  long by  $36\mu$  wide, mostly about  $86.6 \times 36\mu$ , if lateral  $28.6-61.8\mu$  by  $21.7$  to  $26.9\mu$ , mostly about  $44.25 \times 26.9\mu$ . Zoospore formation and sporangium development are of the *P. palmivora* type and a vesicle is usually formed at the end of an exit tube. Zoospores biciliate, spherical to reniform and measuring  $10.3$  to  $14.4\mu$  when resting. Oogonia borne on short side branches, spherical,  $15.5-22.4\mu$  in diameter, occasionally up to  $30\mu$ , with sharp spines of various lengths, measuring up to  $3.6\mu$  long. Eggs single, almost filling the oogonium, measuring  $13.8\mu$  to  $17.2\mu$ , mostly about  $14.3\mu$  to  $15.5\mu$ . The walls of young oogonia present a yellowish brown color, becoming more hyaline at maturity. Mature eggs have a single large eccentric oil globule. Antheridial branches arise either from the same or adjoining hyphae to the oogonium, but most often arise only a short distance below the oogonium. Antheridia single, club-shaped, much larger than the antheridial branch,  $7.0-10.4\mu$  thick. The antheridium is most frequently attached near the stalk. Because of its position, the oogonium often appears to have grown up through the antheridium. The contents of the antheridium are emptied into the oogonium and antheridia attached to mature eggs are entirely empty.

Collected once on petals of *Rhododendron maximum* which had fallen into a cold spring in front of Mr. Mell's cabin near Highlands, North Carolina, in August, 1937.

Rosenbaum (1917) in working out his classification of the genus, separated the species into three groups according to the type of antheridium present. In his first group, the *cactorum* group, the antheridium is said to be attached to the side of the oogonium (paragynous). In his second group, the *phaseoli* group, the antheridium is said to be attached at the base of the oogonium (amphigynous). The oogonium in this group is thought to grow up through the antheridium and then develop, leaving the antheridium as a collar around its base. Since Pethybridge (1913) demonstrated this phenomenon, it has been shown for several species by other workers and has been supported by the cytological investigation of Murphy (1918). In his third group, the *faberi* group, Rosenbaum places all species in which antheridia are unknown.

There seems to be some disagreement as to the accuracy in placing some species either in the *cactorum* group or the *phaseoli* group. *Phytophthora cactorum*, for instance, has been shown to possess both paragynous and amphigynous antheridia. The question has also been raised by Fitzpatrick (1930) as to whether oogonia in the *cactorum* group actually grow up through antheridia, or whether the antheridium is found in a basal position because it coils around the base of the oogonium as has been shown by Cooper (1928) and by Cooper and Porter (1928). Cooper has studied *P. cactorum*, *P. erythroseptica*, *P. richardiae*, and *P. terrestris* in addition to *P. paeonae* and has found this to be the case for all of these species. Earlier investigations on some of these same species and on several others had led to the belief that the oogonium grew up through the antheridium, and although this phenomenon was very unusual, it had been accepted. Observations on *P. stellata* substantiate the observations of Cooper and it is possible that more detailed studies on the early development of other members of this genus will show that the antheridium coils about the base of the oogonium rather than the latter growing up through it.

Most antheridia of *P. stellata* upon first examination appear to be of the amphigynous type, but careful focusing and study with good optics reveal the fact that antheridia in this species coil around the base of the oogonia as is often the case in *P. paeoniae*. Careful study of developing stages bear this out very clearly.

#### THE DEVELOPMENT OF THE SEXUAL ORGANS OF *P. stellata*

For the study of the development of the sexual organs of this fungus, cultures grown on hempseed in distilled water and cultures growing

on maltose-peptone agar #5 were used. The course of development on either medium was identical. The oogonia, when developing in water on hempseed cultures, possess longer and more pointed spines than do those produced in the agar. Those in agar are also slightly larger and the antheridium is smaller than those produced in water. Development was followed both in agar and in water on hempseed, but most of the figures were made from agar cultures. Development in water was terminated if a cover glass were placed over the culture, so it was more difficult to get a good series of developmental stages for figures from these cultures.

The earliest stages in the development that can be recognized are short side branches that have parted so that the two branches appear of about equal length. The one branch seems to grow slightly more rapidly than the other. After growing a short distance, these two branches approach each other. Sometimes they just come in contact but more commonly the one tends to coil around the other (fig. 12) and then soon enlarges (figs. 1 and 13). This branch that coils around the other and enlarges first is destined to form the antheridium. The development of the antheridium in this species seems always to precede slightly the development of the oogonium. The oogonium does not enlarge until after the attachment of the antheridium has taken place. Figs. 2, 6, and 14 show young stages in the early development of oogonia. The protoplasm in the threads and in the young reproductive branches contains many small refractive oil globules.

Sometimes the primary reproductive branches do not grow toward each other but put out secondary branches that come together and develop into antheridia and oogonia (fig. 2). This type of development, as shown in fig. 2, resembles slightly some figures of early stages in development of members of the *erythroseptica* group. In figure 2 it is clear, however, that the antheridium coils around the young oogonial initial rather than the latter growing up through the antheridium. Figures 4, 5, 6, 7, and 15 show early stages in the development of sexual organs and show clearly that the antheridium is coiled about the base of the developing oogonium.

As the antheridium and oogonium develop the protoplasm flows into them, particularly into the oogonium, and appears quite dense and somewhat foamy. As the oogonium approaches its mature size, protuberances grow out at various places over its surface (figs. 8, 9, 16, and 17). The walls of these are at first very thin and the cytoplasm in them is more hyaline and much less granular than that occupying the



central part of the oogonium (figs. 17, 18). These protuberances continue to elongate and become the spines on the wall. In water cultures these spines become very sharp-pointed, but in agar cultures they seldom have such sharp apices.

As the spines are developing on the oogonium, the protoplasm in the center of the oogonium seems to shift position slightly from time to time. These changes in position seem to have no significance. At times more hyaline cytoplasm appears to surround the more densely granular protoplasm. By the time the spines have reached their full length, a thin membrane has formed around the more dense protoplasm of the oogonium (fig. 19) and the antheridium has previously been cut off from the antheridial branch by a cross wall (figs. 18 & 19). In this condition, after the thin membrane is formed around it, the young oosphere is ready for fertilization. Young oospheres commonly lie close to the oogonial wall just opposite the antheridium (figs. 19, 20, and 21).

A very short fertilization tube now grows in from the antheridium and presses against the oosphere membrane. Finally the membrane ruptures and the antheridium discharges its contents into the oogonium. If the antheridium and oogonium are in a median focal plane, a path through the cytoplasm of the young oosphere from the end of the fertilization tube toward its center can be detected (fig. 23). This stage is hard to find as oogonia and antheridia in the correct relationship for this observation are scarce. Of the many developing oogonia watched, I was able to detect this faint fertilization path only three times. Usually all of the antheridial contents pass into the oogonium, but sometimes a few granules are left behind and disintegrate (figs. 24, 20, 21, 25, and 26).

After fertilization the oosphere forms a wall about itself. This wall in the mature condition is made up of two layers of about equal thickness. As the wall is forming, the small oil globules in the oosphere begin to coalesce to form larger oil globules (figs. 20 and 24). These finally all unite into a single slightly eccentrically placed oil globule (figs. 21, 25, 26), a condition characteristic of mature eggs. Germination of the eggs has not been observed.

#### SPORANGIAL DEVELOPMENT

It was difficult for some time to get many sporangia to complete their development and liberate zoospores at ordinary laboratory temperature (77°F.). It was then suggested that young cultures might mature

sporangia if placed in the ice box where the temperature would be somewhat lower (48°F.). Under these conditions sporangial development was normal and often cultures containing developing sporangia when placed in the ice box could be found liberating zoospores after being in the ice box from one and one-half to two hours. When cultures were taken out to be examined, zoospore formation would be retarded after a short time at room temperature, but continued spore formation could be brought about by placing cultures back in the ice box. Sometimes as short a time as fifteen minutes back in the ice box would be sufficient to bring about normal sporangial development again. Sporangia formed at room temperature go into a dormant condition and are characterized by having one or more large oil globules (figs. 30, 31). Sporangia may remain in this condition for several days or longer. If cultures containing resting sporangia are placed in the ice box over night, many sporangia can be found in the morning developing normally and liberating zoospores.

Sporangia of this species are typically obpyriform in shape and may be borne either terminally or on short side branches (fig. 27). The terminal sporangia are considerably larger than the ones borne on lateral branches and are more elongated (figs. 27, 29, 30, 31, 32). The course of sporangial development is of the type described by Butler (1907) for *Phytophthora* (*Pythium*) *palmivora* and in some cases very closely approaches the course of spore liberation and development found in the genus *Pythium*. Forms in which the sporangial contents have been freed into a vesicle entirely undifferentiated and forms in which the zoospores are liberated into the vesicle almost completely formed have been observed.

The stages in the development of the sporangium and the formation of the zoospores are so nearly identical with similar stages figured by Butler (1907) for *P. palmivora* and by Rosenbaum (1917) for *P. arecae* that a detailed account for this species seems unnecessary. Figures 28, 35, 36, 37, 38, show stages in spore formation and escape. In this species a cylindrical exit tube is produced and at the end of this tube the vesicle is formed (fig. 38). This tube may be several microns long or be almost entirely absent. Zoospores are reniform to spherical in shape and measure 10.3–14.4 $\mu$  long. The zoospores possess two cilia of about equal length, which are attached laterally at the hilum (fig. 39).

Sporangia that do not mature zoospores often germinate to form secondary sporangia. This is particularly true in the case of young sporangia when environmental conditions have been altered before the

septum has been formed. After spores have been liberated, proliferation of new sporangia from the base of the old sporangia often takes place. A secondary sporangium has never been observed within the first, but the secondary sporangium is formed at the end of a long stalk which grows out through the exit tube of the old sporangium (fig. 34).

#### TAXONOMIC CONSIDERATIONS

Fitzpatrick (1923, 1930) has shown that the line of demarcation between the genera *Pythium* and *Phytophthora* is very questionable and he suggests that perhaps further investigations of these genera will result in the combining of the two. De Bary (1876), in establishing the genus *Phytophthora*, realized the close affinity of this genus to *Pythium*, but separated the two on their slightly different methods of sporangial germination. In *Pythium*, Butler (1907), Matthews (1931) and others consider that the zoospores are regularly formed in a vesicle, while in *Phytophthora* they are thought to be fully formed within the original sporangium, even in cases when they are emptied into a vesicle. It has been shown that there is no clearly cut distinction between the method of sporangial germination in the two genera (Butler, 1907, and Rosenbaum, 1917), and that in *Phytophthora* sporangial germination typical of *Pythium* occurs. Fitzpatrick (1930) says: "The shape of the sporangium in most species of *Pythium* may be said to be characteristically more nearly spherical than in *Phytophthora* where it is usually oval to obpyriform and papillate, but so many integrating conditions exist that shape has only relative diagnostic value. Buisman summarizes the situation with the statement that although theoretically no sharp line can be drawn between the two genera, it is usually possible in practice to determine whether a given form belongs to the *Phytophthora* type or to the *Pythium* type."

In deciding whether the present plant was a *Pythium* or a *Phytophthora*, the author realized the fact that often the type of sporangial development strongly suggests *Pythium*, but felt that the shape of the sporangia and the presence of a papilla indicated that it was a *Phytophthora* whose sporangial germination shows a close relationship to *Phytophthora palmivora* Butler. Butler (1907) at first considered *P. palmivora* as *Pythium palmivorum*, but later concluded that his plant was a *Phytophthora* (Sharples and Lambourne, 1922).

#### SUMMARY

1. A new species of *Phytophthora* with spiny oogonia is described and named *P. stellata*.

2. The development of the sexual organs of this species is discussed and a comparison is made with methods known for other members of the genus.

3. Sporangial development and zoospore formation are considered and compared with that of other species of *Phytophthora* and with *Pythium*.

4. The taxonomic relationships of this species are brought out and in its sporangial development this species is shown to be closely related to *P. palmivora* Butler.

DEPARTMENT OF BOTANY,  
UNIVERSITY OF NORTH CAROLINA,  
CHAPEL HILL, NORTH CAROLINA.

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### EXPLANATION OF PLATES

#### PLATE 15

- Figs. 1-9. Early stages in development of antheridia and oogonia. Figs. 1-5 from agar cultures; 6-9 from water cultures growing on hemp seed.  $\times 505$ .
- Figs. 10 & 11. Surface views of two reproductive branches showing general appearance. Fig. 10 from water culture; fig. 11 from agar culture.  $\times 505$ .
- Figs. 12-21. Stages in development of sexual organs. Fertilization took place between 19 & 20. The contents of antheridium could not be followed because of the position of the organs but a gradual decrease in antheridial contents could be observed. From an agar culture.  $\times 505$ .
- Figs. 22-24. Stages in fertilization. Fig. 22 shows penetration of fertilization tube through oogonial wall and pressing against oosphere membrane. Fig. 23, a median optical section showing the contents of antheridium passing into oosphere and through oosphere cytoplasm. Faint indications of an ooplasm and a periplasm can be seen in the oosphere. Fig. 24 shows a little later stage in which a wall is forming and a few protoplasmic granules can be seen disintegrating in the antheridium.  $\times 830$ .
- Figs. 25-26. Mature eggs in oogonia from water cultures.  $\times 505$ .

#### PLATE 16

- Fig. 27. Habit sketch of a portion of a hypha showing numerous sporangia and a reproductive branch.  $\times 83$ .
- Fig. 28. Early stage in formation of a sporangium.  $\times 367$ .
- Figs. 29-31. Terminal sporangia. Figs. 30 & 31 resting conditions showing large oil globules.  $\times 367$ .
- Figs. 32-33. Lateral sporangia; fig. 33 forming exit tube previous to spore formation.  $\times 367$ .
- Fig. 34. Showing proliferation of a second sporangia from base of older empty one.  $\times 175$ .
- Fig. 35. Empty sporangium showing exit tube.  $\times 367$ .
- Figs. 36-38. Stages in sporangial germination.
- Fig. 39. Zoospores, (a) resting condition.  $\times 367$ .

# PLATE 15

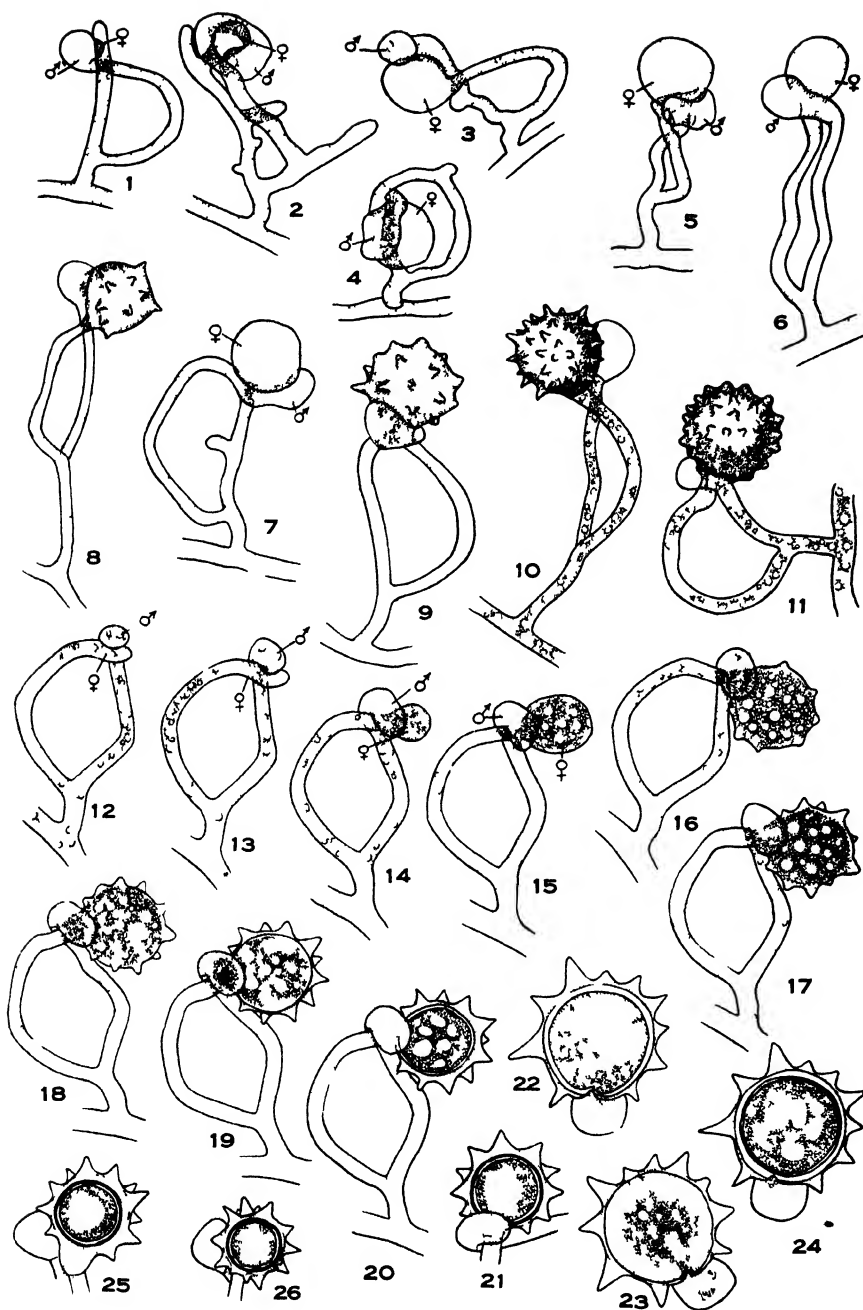
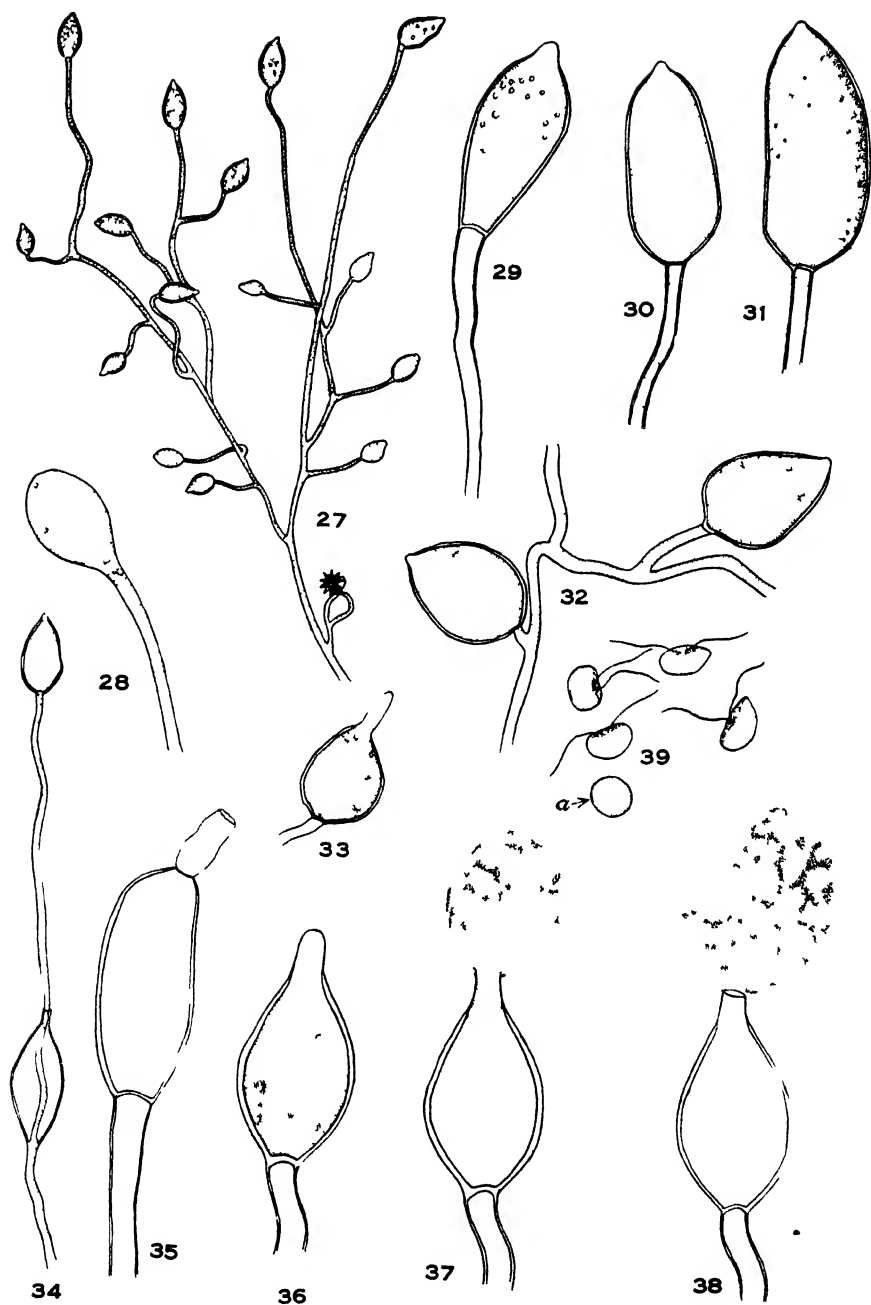




PLATE 16







JOURNAL  
OF THE  
Elisha Mitchell Scientific Society

Volume 54

December, 1938

No. 2

PROCEEDINGS OF THE THIRTY-SEVENTH ANNUAL  
MEETING OF THE NORTH CAROLINA ACADEMY  
OF SCIENCE

NORTH CAROLINA STATE COLLEGE OF AGRICULTURE AND ENGINEERING  
OF THE UNIVERSITY OF NORTH CAROLINA, RALEIGH, N. C.,  
MAY 6 AND 7, 1938

The thirty-seventh annual meeting of the North Carolina Academy of Science was held at the North Carolina State College of Agriculture and Engineering of the University of North Carolina, May 6 and 7, 1938. The meeting was called to order at 9:30 A.M. on May 6 by the President, W. E. Speas. The President called for the reading of papers which continued until 11:00 A.M. when he appointed the following committees:

Auditing: A. A. Dixon, I. V. Shunk, R. N. Wilson.

Resolutions: J. P. Givler, J. N. Couch, H. E. Fulcher.

Nominating: H. R. Totten, Bert Cunningham, J. B. Derieux.

The reading of papers was then resumed and continued until 1:30 P.M. when recess was taken for luncheon.

The afternoon meeting commenced at 2:15 P.M. and met in two sections: the General Section and the Botanical Section. The reading of papers in these sections continued until 4:30 P.M. when the Academy held its annual business meeting.

The minutes of the previous meeting were approved as published in the *Journal of the Elisha Mitchell Scientific Society* after the following correction was made: on page 218 the third and fourth lines from the bottom should read, *Mathematics Section*: Chairman, Archibald Hen-

derson, The University of North Carolina; Secretary, J. J. Gergen, Duke University.

Reports from the various committees were presented.

The executive committee, consisting of W. E. Speas, president of the Academy; M. L. Braun, vice-president; H. L. Blomquist, secretary-treasurer; H. R. Totten, W. L. Porter, and R. F. Poole, reported as follows:

"The executive committee met in Raleigh on May 5 and again on May 7. The following matters were taken up by the committee:

"(1) Officers were appointed for the temporary sections of Botany and Zoology: For the Botany Section, B. W. Wells, chairman; Ruth M. Addoms, secretary; for the Zoology section, Bert Cunningham, chairman; O. C. Bradbury, secretary.

"(2) The committee suggested that at the Saturday morning meetings of the temporary sections the members of each section decide whether to elect officers themselves within the respective sections or leave it to the executive committee to appoint the officers should the program become so crowded another year that it would be necessary to set up temporary sections.

"(3) The committee reported as elected to membership since the last meeting the following:

Baer, Reinhold, Dept. of Mathematics, U. N. C., Chapel Hill, N. C.

Brown, Frank H., Dept. of Chemistry, Western Carolina Teachers College, Cullowhee, N. C.

Burling, L. D., Dept. of Geology, U. N. C., Chapel Hill, N. C.

Clegg, R. E., Dept. of Chemistry, N. C. State College, Raleigh, N. C.

Collins, E. R., Dept. of Agronomy, N. C. State College, Raleigh, N. C.

Conant, Norman F., Duke Hospital, Durham, N. C.

Cook, Freeman W., Dept. of Poultry, N. C. State College, Raleigh, N. C.

Cox, Hiden T., Dept. of Botany, U. N. C., Chapel Hill, N. C.

Doubles, James A., Dept. of Botany, U. N. C., Chapel Hill, N. C.

Evans, M. M., Dept. of Plant Pathology, N. C. State College, Raleigh, N. C.

Fornes, Gaston G., School of Engineering, N. C. State College, Raleigh, N. C.

Fountain, A. M., Dept. of English, N. C. State College, Raleigh, N. C.

Gardner, W. S., Jr., Soils Laboratory, N. C. Highway Dept., Raleigh, N. C.

Gravett, Howard S., Dept. of Biology, Elon College, Elon, N. C.

Hackney, J. Carlyle, Dept. of Chemistry, N. C. State College, Raleigh, N. C.

Harvey, P. H., Dept. of Plant Breeding, N. C. State College, Raleigh, N. C.

Highsmith, J. Henry, State Dept. of Public Instruction, Raleigh, N. C.

Hinkle, L. E., Dept. of Languages, N. C. State College, Raleigh, N. C.

Irwin, W. H., Dept. of Geology, U. N. C., Chapel Hill, N. C.

Jacobson, Nathan, Dept. of Mathematics, U. N. C., Chapel Hill, N. C.

Jensen, Henry W., Asheville Farm School, Swannanoa, N. C.

Johnson, M. W., Dept. of Zoology, Duke University, Durham, N. C.

- Kime, P. H., Dept. of Plant Breeding, N. C. State College, Raleigh, N. C.  
Logan, Thomas S., Dept. of Chemistry, Davidson College, Davidson, N. C.  
Lovvorn, R. L., Dept. of Agronomy, N. C. State College, Raleigh, N. C.  
Mack, Edward, Jr., Dept. of Chemistry, U. N. C., Chapel Hill, N. C.  
Mankin, W. D., Spencer Lens Co., Washington, D. C.  
Melich, Adolph, Dept. of Chemistry, N. C. State College, Raleigh, N. C.  
Middleton, G. K., Dept. of Plant Breeding, N. C. State College, Raleigh, N. C.  
Nahikian, Howard M., Dept. of Mathematics, N. C. State College, Raleigh, N. C.  
Olive, Lindsay S., Dept. of Botany, U. N. C., Chapel Hill, N. C.  
Olivera, Fernando, Dept. of Plant Pathology, N. C. State College, Raleigh, N. C.  
Owens, O. P., Dept. of Plant Pathology, N. C. State College, Raleigh, N. C.  
Parkinson, Leslie R., School of Engineering, N. C. State College, Raleigh, N. C.  
Poplin, R. L., Dept. of Chemistry, Campbell College, Buies Creek, N. C.  
Rafik, Ahmad, Dept. of Agronomy, N. C. State College, Raleigh, N. C.  
Rankin, W. B., Dept. of Chemistry, N. C. State College, Raleigh, N. C.  
Rankin, W. H., Dept. of Agronomy, N. C. State College, Raleigh, N. C.  
Rice, Oscar K., Dept. of Chemistry, U. N. C., Chapel Hill, N. C.  
Rigler, Neil E., Dept. of Agronomy, N. C. State College, Raleigh, N. C.  
Ritchie, Lawrence, Dept. of Biology, W. C. of U. N. C., Greensboro, N. C.  
Ryder, Eleanor, Dept. of Biology, Catawba College, Catawba, N. C.  
Savely, Harvey E., Dept. of Zoology, Duke University, Durham, N. C.  
Schumacher, F. X., School of Forestry, Duke University, Durham, N. C.  
Setzer, Elsie G., Dept. of Botany, U. N. C., Chapel Hill, N. C.  
Shad, Fred, Dept. of Chemistry, Davidson College, Davidson, N. C.  
Shanklin, J. A., Dept. of Agronomy, N. C. State College, Raleigh, N. C.  
Singer, Wm. E., Dept. of Chemistry, N. C. State College, Raleigh, N. C.  
Stuart, A. D., Dept. of Agronomy, N. C. State College, Raleigh, N. C.  
Stupka, Arthur, Great Smoky Mts. Nat. Park, Gatlinburg, Tenn.  
Sutton, P. P., Dept. of Chemistry, N. C. State College, Raleigh, N. C.  
Tillery, Doris, Dept. of Mathematics, Meredith College, Raleigh, N. C.  
Van Leer, Blake R., School of Engineering, N. C. State College, Raleigh, N. C.  
Ward, Mary W., Dept. of Botany, U. N. C., Chapel Hill, N. C.  
West, Gladys F., Cotton Fiber Laboratory, N. C. State College, Raleigh, N. C.  
Wharton, George W., Dept. of Zoology, Duke University, Durham, N. C.  
Whiffen, Alma J., Dept. of Botany, U. N. C., Chapel Hill, N. C.  
Wicker, Dan B., School of Engineering, N. C. State College, Raleigh, N. C.  
Williams, Carlos F., N. C. Agricultural Experiment Station, Raleigh, N. C.  
Wilson, A. J., Dept. of Chemistry, N. C. State College, Raleigh, N. C.  
Wilson, Myrtle, M., Dept. of Botany, N. C. State College, Raleigh, N. C.  
Zoology Field Club, Dorothy Bell, Sec., W. C. of U. N. C., Greensboro, N. C.

"(4) The following former members were re-instated to membership:

Brannon, C. H., Dept. of Entomology, N. C. State College, Raleigh, N. C.  
 Carpenter, D. W., Dept. of Physics, Duke University, Durham, N. C.  
 Eliason, Nancy, Meredith College, Raleigh, N. C.  
 Gray, I. E., Dept. of Zoology, Duke University, Durham, N. C.  
 Howell, Thelma, Dept. of Biology, Wesleyan College, Macon, Ga.  
 Lutz, J. F., Dept. of Agronomy, N. C. State College, Raleigh, N. C.  
 McDearman, Ella, W. C. of U. N. C., Greensboro, N. C.  
 Mouzon, J. C., Dept. of Physics, Duke University, Durham, N. C.  
 Ramsey, George R., Dept. of Chemistry, Catawba College, Salisbury, N. C.  
 Reid, W. A., Dept. of Chemistry, N. C. State College, Raleigh, N. C.  
 Rhodes, L. B., Dept. of Agronomy, N. C. State College, Raleigh, N. C.  
 Stuhlman, Otto, Dept. of Physics, U. N. C., Chapel Hill, N. C.  
 Trentham, S. O., Mars Hill College, Mars Hill, N. C.  
 Williams, L. F., Dept. of Chemistry, N. C. State College, Raleigh, N. C.  
 Wray, D. L., Dept. of Agriculture, N. C. State College, Raleigh, N. C.

"(5) The committee also reported the following losses during the year:

Lost by death: Dr. W. L. Poteat, Mrs. B. W. Wells.

Lost by resignation: James W. Culbertson.

Dropped from the roll because of non-payment of dues, 32 former members.

The Treasurer's report was as follows:

*Financial Statement of the N. C. A. S., May 5, 1938*

*Receipts*

Balance on hand May 7, 1937:

Savings Account.....	\$348.65
Checking Account.....	151.41
Cash on hand.....	8.00

\$508.06

Dues:

1936.....	2.00
1937.....	164.00
1938.....	210.00

Initiation fees:

1937.....	34.00
1938.....	62.00

472.00

Interest on Savings.....

8.76

Total receipts.....

\$988.82

*Disbursements*

Stationery and printing.....	26.48	
Programs, 1938.....	32.50	
Postage.....	4.03	
Refund dues.....	6.00	
Books for H. S. Essay prize 1937.....	14.79	
Express on books to prize winner.....	.45	
Journal of E. M. S. S., 1937.....	300.00	
Charges on bank balance.....	.23	
Clerical assistance.....	53.00	
Sec.-treas. Commission.....	47.20	
Refund Sec. dues.....	2.00	
Sec. expenses to 1937 meeting.....	5.00	
Telegrams.....	.32	
Telephone calls.....	.60	
Receipt books.....	1.04	
Money order.....	.10	
Reprints from J. E. M. S. S.....	11.25	
		<hr/>
Total disbursements.....		504.99
		<hr/>
Total balance May 5, 1938.....		\$483.83

*Savings Account*

Balance May 7, 1937.....	\$348.65	
Interest July, 1937, and April, 1938.....	8.76	
		<hr/>
Balance May 5, 1938.....	\$357.41	357.41
		<hr/>
Cash on hand (dues).....		\$126.42
		<hr/>
May 5, 1938—Balance in checking account.....		8.00
		<hr/>
		\$118.42

The above report was made as of May 5, 1938.

Submitted by H. L. Blomquist, Secretary-Treasurer.

Audited May 6, 1938, by

A. A. Dixon

I. V. Shunk

R. N. Wilson.

The committee accepted the invitation of the faculty of Wake Forest College to hold the thirty-eighth meeting of the Academy at Wake Forest.

The executive committee made the following recommendations to the Academy:

1. That all bills presented in the Treasurer's report be authorized and paid and that the report be printed when audited.

2. That Bert Cunningham be appointed to select the books to be presented to the winner of the High School Science Essay Prize and that he be authorized to draw upon the Treasurer for \$20.00 for these books; and that the Secretary be authorized to appoint a representative of the Academy to award the prize and draw upon the treasury for the payment of his expenses.

3. That the Secretary-Treasurer be authorized to pay the Elisha Mitchell Scientific Society \$300.00 for the publication of the 1938 Proceedings.

4. That the Academy issue membership cards which the Secretary send to the members of the Academy in good standing.

5. That the Constitution of the Academy be amended as follows: Article II, Section I, be amended by the following:

"Article II, Section I. Membership shall be of three kinds:

(a) Any person actively interested in science or the promotion of science, may, upon nomination by two members, be elected a member of the Academy by a majority vote of the executive committee, and shall be entitled to all privileges of the Academy. (b) Active organizations having scientific objectives may upon application, acceptance by the executive committee, and the payment of a fee of \$2.00 become an affiliate of the Academy for the current year. The affiliation may be renewed year by year by the executive committee upon receipt of the affiliation dues of \$2.00 per year. Affiliated organizations shall be entitled to receive the Journal and such notices as are issued to the members of the Academy, and each such affiliated organization shall be entitled to elect a delegate to the Academy who shall have the right to vote in all meetings."

The report of the executive committee and its recommendations were accepted and approved by the Academy.

The auditing committee reported that the Treasurer's report had been examined and was found to be correct.

The reports of the Treasurer and the auditing committee were accepted.

The committee on the Academy Medal awarded the gold medal for 1938 to F. H. Prytherch of the U. S. Bureau of Fisheries, Beaufort,

N. C., for his paper entitled "Life Cycle of a Sporozoan Parasite of the Oyster" which was considered the most noteworthy paper presented at the thirty-seventh meeting of the Academy.

The committee on high school science, consisting of Bert Cunningham, chairman, H. B. Arbuckle, C. E. Preston, R. J. Campbell, Mary Conrad Clever, and J. H. Highsmith, reported as follows:

"The committee reports that it conducted the usual essay contest and that the judges, R. N. Wilson, O. J. Thies, and W. E. Speas selected Mr. Larry Hardin of the Boyden High School at Salisbury, N. C., as the winner of the prize. It recommends that the chairman of the committee be authorized to purchase not more than \$20.00 worth of books as the award and that the secretary of the Academy be authorized to select a member of the Academy to deliver the prize.

"The committee feels that the essay contest has not been so successful as we had hoped. Other methods of interesting high school students were suggested. The details have not been worked out, but the committee recommends that it be granted the same amount of money for an award next year.

"The committee also reports that it canvassed a number of high school teachers as to the desirability of a meeting primarily for them at the time of the Academy meeting. The responses were especially gratifying. While we were unable to arrange a program for this year, we believe it can be done another year. The committee recommends that it be authorized to proceed. In the committee meeting other plans were discussed but they need further consideration before recommendations can be made.

"The committee urges members of the Academy to attend the district meetings of the N. C. E. A. and take part in the discussions. This would provide an unusual stimulus to the high school teachers."

The report of the high school science committee was accepted and its recommendations approved.

The legislative committee had no report to make this year.

The elective appraisal committee reported that, as there had been no requests for appraisals, there was no report to present.

The conservation committee made the following report:

"Last winter a letter from Dr. A. O. Weese, Chairman of the Committee on the Preservation of Natural Conditions for the United States of the Ecological Society of America was referred to this committee for attention and action. His letter, dated January 10, extends—"to the North Carolina Academy of Science an invitation to join in the work



of the Committee on Preservation of Natural Conditions." We were further informed that this committee included a local group in each state, the local member in North Carolina being Dr. B. W. Wells. Dr. Wells was thereupon consulted and though he did not definitely express an opinion on the question at issue, namely the affiliation of the Academy with the Ecological Society, he showed that he was deeply interested in and fully conversant with objects of the committee; in fact, he named a number of places where natural areas should be established.

"At a meeting of the conservation committee at Duke University, February 28, at which Drs. W. C. Coker, C. F. Korstian, H. J. Oosting and the Chairman were present, the matter was thoroughly discussed and all those present were heartily in favor of some action by the Academy to increase interest in the conservation of natural conditions and in the acquisition and dedication of outstanding natural areas in the public interest. As examples of such outstanding areas which are in great need of protection from devastation and the probable obliteration of natural conditions which should by all means be preserved, not only for scientific but for aesthetic purposes, are the following:

"1. Smith Island. This is the northern limit of the cabbage palmetto and its only occurrence in North Carolina. Efforts have been made in the past to acquire this island but the necessary funds could not be found. It has recently passed into the hands of a well-to-do North Carolinian who plans to develop it. An effort to reserve a part of it as a public park might still be successful.

"2. The virgin forest tract at Highlands, N. C., owned by the Ravenel family. This tract is said to contain the largest specimens of six of North Carolina's principal tree specimens amongst which are the Canada hemlock and the cucumber tree. There was some thought that the United States Forest Service would acquire this to add to the Nantahala National Forest for retention as a natural area and there is still a possibility of this if and when funds can be made available.

"3. The Big Savannah (or similar area). This is an area destitute of trees, lying in Pender County. It is noted for the large variety of flowering plants that occur upon it. It has been subject to annually recurring fires which have kept down shrubbery and tree growth. A limited area within a short distance of the hard-surfaced road between Wilmington and Goldsboro might well be dedicated to such use. Such a natural area would form a most attractive point for tourists as well as for scientists.

"4. Roan Mountain. On the summit of this high mountain on the boundary between North Carolina and Tennessee are hundreds of acres of open grassland with enormous clumps of rose rhododendron scattered about with similar areas of southern balsam, mountain alder and other mountain species. Lumbering has destroyed much of the forest surrounding the open land and much rhododendron has been dug for the commercial trade. The effort to save what is left should be pushed until successful.

"5. An area in southeastern North Carolina should be secured for the perpetuation of the Venus Fly Trap. Unfortunately the city of Wilmington or some of its commercially-minded citizens are capitalizing on this rare plant and shipping it long distances for no better reason than that someone is willing to pay for it. It might be possible to combine this with the No. 3, the Big Savannah, although a separate area would probably best meet the need.

"Other areas which have been recommended as natural areas are Buck Forest in Transylvania County, where the Hartford Fern (*Lygodium palmatum* (Bernh.) Sw.) and other rare plants thrive; Paint Rock in Madison County, where the rare *Buckleya distichophylla* (Nutt.) Torr. and four species of *Magnolia* occur; Tennessee Bald, which will be on the Park to Park Highway; and an area in the heart of Angola Bay in Duplin County as yet unharmed by man.

Some little has already been accomplished towards securing natural areas. According to the Regional Forester in charge of the National Forests in this Southern Region:

"The Joyce Kilmer Memorial Forest in Graham County is the only actually established natural area in North Carolina. This area is, strictly speaking, a memorial but is comparable to and serves the purpose of a natural area and could be so called.

Another area surrounding the Joyce Kilmer Forest and extending across the state line into the Cherokee National Forest, known as the Citico-Cheoah Primitive Area, has been suggested and reported on, but the report was returned to the Supervisor for revision and the area has not yet been established.

Both natural areas and primitive areas are established by action of the Chief, after recommendation by the Regional Forester, under Regulation L-20. Under this regulation, no occupancy under special use permit is allowed, or the construction of permanent improvements by any public agency permitted, except as authorized by the Chief or the Secretary of Agriculture.

Natural areas differ from primitive areas in that their purpose is to preserve in an unmodified condition areas representative of the virgin growth of the forest and related influences, to the end that they will be

available for science, research, and education. The cutting of timber, grazing, or similar uses are prohibited. Scientific and educational use prevail and general public use is restricted or prohibited.

Primitive areas are set up for purposes best described by their name. Primitive conditions of transportation, subsistence, habitation, and environment are the aims in their management. Industrial utilization of resources, however, is not prohibited, but is properly regulated by a management plan for the area. Road or trail construction is held to a minimum required by the management plan. Occupancy under special use permit is also held to a minimum."

"The Black Mountain Natural Spruce Area on the Mount Mitchell Division of the Pisgah National Forest in Yancey County was reported to the Chief of the United States Forest Service in 1933, but no further action has been taken in establishing this area. A resolution from this Academy, endorsing this project and urging early and favorable action by the Chief Forester could, this committee feels, be very appropriate.

"There are no doubt other natural areas within our National Forests or the Smoky Mountains National Park which could be similarly dedicated without any transfer of title. The same is true of our State Parks and one of these, the Hanging Rock State Park in Stokes County, has many unique features. It is the present policy of the State Department of Conservation and Development to administer these parks not only as wild-life sanctuaries but as natural areas. The administration of desirable natural areas might well be entrusted to a state organization which emphasizes the conservation of its animal and plant life.

"The question to be considered by this Academy, however, is not whether we favor the acquisition of natural areas and their permanent protection by some interested public agency, but it is whether we can with advantage to ourselves and the Ecological Society of America cooperate with them in forwarding such a program for North Carolina. Dr. Weese says:

"If the North Carolina Academy of Science elects to contribute any amount from \$2.00 up as dues, it may become a contributing member of the Ecological Society and on this account will receive the bulletin of the Society and such reports of conditions as are published separately. If it designates that its membership fees be used for the purposes of the Committee on Preservation of Natural Conditions it will in that way become affiliated with the Committee. It would then be entirely fitting that it elect a member of the State Committee."

"While our program for the dedication of natural areas in North Carolina will of course depend in large part upon the activities of the

Academy, the example and inspiration of a nation-wide organization engaged in the same beneficent work might well be helpful. It would certainly seem to be worth \$5 or \$10 even if Dr. Weese's invitation were accepted experimentally. Your Committee therefore recommends that with the Approval of the Executive Committee a \$5 or \$10 contribution be made to the Ecological Society designating that it be used for the purpose of the Committee on the Preservation of Natural Conditions."

W. C. COKER,  
J. P. GIVLER,  
C. F. KORSTIAN,  
H. J. OOSTING,  
J. S. HOLMES,  
*Committee.*

The report was accepted and approved.

Following this report the Chairman, J. S. Holmes, read the following resolutions:

#### "RESOLUTION I

"Whereas the United States Forest Service seems to have taken the lead in the establishment and protection of natural areas in North Carolina, and

"Whereas no progress seems to have been made on the approval of the Black Mountain Natural Area since its recommendation in 1933, and

"Whereas the Ravenel Virgin Forest at Highlands, Macon County, is undoubtedly one of the finest natural areas in the eastern United States and has been recommended for acquisition by the United States Forest Service for inclusion in the Nantahala National Forest.

"Therefore be it **RESOLVED** that the North Carolina Academy of Science in annual session does earnestly request the Chief Forester of the United States Forest Service to do everything possible to dedicate the Black Mountain area and to acquire and administer as a Natural Area the Ravenel Forest at Highlands."

#### "RESOLUTION II

"**RESOLVED** that the North Carolina Academy of Science accept the invitation of the Ecological Society of America and contribute the sum of \$5 towards the work of the Committee on the Preservation of Natural Conditions, with the understanding that such contributing

membership may be discontinued by majority vote at any annual business meeting."

A motion was made and passed that these resolutions be adopted by the Academy and that the Secretary be instructed to send Resolution I to the Chief Forester of the U. S. Forest Service.

The committee on the A. A. A. S. Research Grant reported that the 1938 grant be recommended to Dr. Henry W. Jensen for his project, "Continuation of a study on the evolution of the dioecious flora of the southern Appalachians with special reference to the function of the chromosomes in sex determination."

The report of the committee on the A. A. A. S. Research Grant was accepted and approved.

Bert Cunningham, representative to the A. A. A. S., reported as follows:

"The general report of the A. A. A. S. has appeared in Science, but your representative wishes to call attention to certain features of the council meetings.

"It is quite evident that the A. A. A. S. wishes to enlarge its membership substantially. To do this several innovations were discussed. (a) Removal of the initiation fee. This was adopted. (b) Establishment of junior membership, especially for high school students. (c) Drive for non-scientific adult membership. The accomplishment of the two latter objectives would necessitate a change in publications of the Association. Science would remain much as it is; The Scientific Monthly would be made to appeal to the non-scientific adult readers; and a third periodical would be established for readers at the high school level. Your representative is of the opinion that after much discussion no definite decision was reached. His own feeling in the matter is that the Association will lose prestige by too great an expansion, especially if there are many immature and non-scientific members. Since there will not be another meeting of the Academy before the A. A. A. S. meeting at which final action will probably be taken, your representative invites your comments by mail.

"The Academy Conference was well attended. The theme of the meeting was—"What have the Academies done with the research grants from the A. A. A. S." Each Academy was expected to present a written report. Thanks to our efficient secretary (H. L. Blomquist) your representative was able to present a report which the executives cited as a model. Your representative was surprised to find that some of the Academies had made no use whatsoever of their grants. Since

a rather considerable number of Academies made no report this will probably be a matter for discussion at the next meeting. Dr. E. C. L. Miller, Chairman, gave an interesting talk on "What next" in which he stressed the desirability of greater recognition of those experimental psychologists who are working on a more scientific basis. In the elections your representative was chosen as vice-chairman for the current year.

"The more useful and efficient services of this Conference in recent years is directly traceable to the activity and interest of the Conference Secretary, Dr. W. J. Bilsing, upon whose shoulders the responsibility for the meetings rest."

The above report was accepted by the Academy.

The following memorial reports honoring the late William Louis Poteat and Mrs. Edna Metz Wells were presented:

#### MRS. EDNA METZ WELLS

"The North Carolina Academy of Science has lost in Mrs. Edna Metz Wells one of its faithful members of long standing and desires to put on record an appreciation of her character and her personality and her work especially in the teaching of high school science. Mrs. Wells came to the state with her husband, Dr. B. W. Wells, in 1919 and soon afterwards joined the Academy of Science. She always took an active interest in the programs of the Academy and was especially interested in the Committee on High School Science of which she was a member since its organization. She was particularly effective in bringing into secondary schools the ideals and objectives of the Academy.

"She rendered enthusiastic and devoted service in the Raleigh high schools for seventeen years. She has been the only real contact with the ideals and accomplishments of science for many hundreds of young men and women, who owe their interest in and present appreciation of the accomplishments of science to her stimulating teaching.

"As fellow members of the Academy of Science, we desire to render respectful homage to the fine qualities of mind and heart possessed by Mrs. Wells. And it is with keen and sorrowful regret that we record the untimely end of so useful a life."

BERT CUNNINGHAM,  
DONALD B. ANDERSON,  
Z. P. METCALF,  
*Committee.*

## WILLIAM LOUIS POTEAT

"In the passing of William Louis Poteat, North Carolina and the South lost an outstanding citizen. His interests were broad and varied. His influence was felt in particular in the fields of education, religion and public morals.

"The North Carolina Academy of Science has sustained a particularly heavy loss. He was one of the founders of the Academy, being present at the first preliminary meeting of this body in the State Agricultural Building at Raleigh on March 21, 1902. Here the Academy was organized and Doctor Poteat was elected as its first President. He presided at the first annual meeting for the presentation of papers, which was held at Trinity College, Durham, November 28 and 29, 1902. At this meeting the subject of his presidential address was "Science and Life." During the thirty-six years of his membership in the Academy, he presented various papers both on specific subjects and broad general ones. His particular interest was in the Thallophyta, including both Algae and Fungi.

"In the field of education Doctor Poteat's influence was felt throughout the South. One of his outstanding contributions was made in respect to academic freedom. The courageous stand that he took throughout many years was one of the main factors in the maintenance of this cardinal principle. The colleges and universities of North Carolina in particular owe him a lasting debt of gratitude for the freedom of teaching that they now enjoy.

"As a teacher Doctor Poteat was unique. From the information at hand it seems that he was the first teacher in the South to give organized laboratory work to classes of students. He served as Assistant Professor of Biology at Wake Forest College from 1880 to 1883, and as Professor of Biology from 1883 to 1938. During the period of his service he awakened and stimulated the interest of his students in the study of nature. He was a natural teacher, attracting and holding the admiration and respect of all who came in contact with him either in the classroom or outside of it. As President of Wake Forest College from 1905 to 1927, he exerted a powerful influence upon the development of higher education in the state. In recognition of his worth many academic honors were conferred upon him by outstanding universities.

"In the field of religion Doctor Poteat's influence was felt deeply. He always insisted that science and religion were entirely compatible; that if any incompatibility appeared to exist, it was because of an incomplete understanding and lack of appreciation of either science or

religion, or both. He combined the two in his teaching, strengthening the one by the other. His preëminence in the religious world was emphasized by his selection by the University of North Carolina to give in 1925 a series of lectures under the McNair Foundation. These lectures were published in book form under the title, "Can a Man Be a Christian Today?" As one of the leaders in religious affairs in the state and the South, he wielded a strong influence for approximately a half century. He was elected President of the North Carolina State Baptist Convention in 1937.

"In addition to his principal interests, namely, religion and education, Doctor Poteat took an active interest in state affairs in respect to temperance, and international affairs in respect to peace, having published a book on each subject, "Stoplight" and "The New Peace."

"Our friend and co-worker was born October 20, 1856, in Caswell County near Yanceyville. He died at his home in Wake Forest March 12, 1938, departing this life in a gentle and peaceful manner, as he had lived for eighty-one years. With his departure, the fields of religion and education and the state lost a valuable friend.

"To his family, The North Carolina Academy of Science extends its deepest sympathy, and makes present acknowledgment of its own deep loss. The Academy directs that this statement be spread upon its minutes and that the Secretary transmit a copy to the bereaved family."

C. S. BLACK,  
W. C. COKER,  
O. C. BRADBURY,  
*Committee.*

A motion was made and seconded that the North Carolina Academy of Science Medal be named in honor of Dr. Poteat the "Poteat Medal." The motion was passed by a unanimous vote.

The president then announced the appointment of the following committees:

Legislative Committee: H. F. Prytherch, chairman, B. W. Wells, W. F. Prouty.

Conservation Committee: J. S. Holmes, chairman, J. P. Givler, C. F. Korstian, W. C. Coker, H. J. Oosting.

High School Science Committee: Bert Cunningham, chairman, H. B. Arbuckle, C. E. Preston, R. J. Campbell, Mary Conrad Clever, J. H. Highsmith.

Committee on the medal award: J. N. Couch, chairman, O. C.



Bradbury, E. W. Berry, Edward Mack, Jr., H. L. Blomquist, J. P. Givler, J. B. Derieux, and O. J. Thies, Jr.

The Elective Appraisal Committee: P. M. Ginnings, chairman, E. H. Hall, R. E. Coker, Mary Conrad Clever, C. W. Edwards, Karl H. Fussler, E. G. Purdom, R. N. Wilson.

The nominating committee submitted the following nominations:

*President:* John W. Lasley, Jr., The University of North Carolina.

*Vice-President:* Donald B. Anderson, North Carolina State College.

*New member on the Executive Committee:* (for three years) O. C. Bradbury, Wake Forest College.

Two new members (for three years) on the *Committee of the A. A. A. S. Research Grant:* M. L. Braun and P. M. Ginnings.

*Representative to the A. A. A. S.:* Bert Cunningham, Duke University.

The nominations were accepted and the Secretary was instructed to cast the ballots for the nominees.

The general resolutions committee made the following report:

"The North Carolina Academy of Science wishes to express its sincere appreciation for the delightful entertainment received at State College. We desire to express our appreciation to the local committee on arrangements, to State College for its complimentary supper, to the State College Woman's Club for the pleasant reception tendered the Academy, and to the students of State College who have so generously assisted with the registration and other routine matters."

H. E. FULCHER,

J. N. COUCH,

J. P. GIVLER,

*Committee.*

The business meeting then adjourned.

At 6:30 P.M. the members of the Academy were entertained at a complimentary supper in Pullen Park, near the N. C. State College Campus.

At 8:30 the evening meeting was held with Vice-president Milton L. Braun presiding. The address of welcome was made by J. W. Harrelson, Dean of the Administration of North Carolina State College. This was followed by the presidential address, "The Father of Nuclear Physics" by the retiring president, W. E. Speas.

After the presidential address an informal reception was extended to the Academy by the State College Woman's Club.

On Saturday morning the Academy met in sections as follows: General Section, Botany Section, Zoology Section, Mathematics,

Physics Section, and the North Carolina Section of the American Chemical Society.

The following officers were elected by the respective sections:

*Chemistry Section:* Chairman, Neville Jones, Wake Forest College; Vice-Chairman, E. C. Markham, The University of North Carolina; Secretary-Treasurer, Ivan D. Jones, North Carolina State College of U. N. C.; Councillors, R. W. Bost, The University of North Carolina; D. G. Hill, Duke University; Members of the Executive Committee, W. C. Vosburgh, Duke University; Edward Mack, Jr., The University of North Carolina; Walter Jordan, North Carolina State College of U. N. C.

*Mathematics Section:* Chairman, R. C. Bullock, North Carolina State College of U. N. C.; Secretary, E. A. Cameron, The University of North Carolina.

*Physics Section:* Chairman, W. E. Speas, Wake Forest College; Secretary, F. W. Lancaster, North Carolina State College of U. N. C.

*Zoology Section:* Chairman, Bert Cunningham, Duke University; Secretary, Z. P. Metcalf, North Carolina State College of U. N. C.

The Botany Section did not elect officers but left the appointment of officers to the Executive Committee.

The following papers were presented. Those marked\* appear in this issue; those marked x are abstracted with the Proceedings; those marked † were read by title.

#### GENERAL SECTION

x*Hydraulic separation of mineral constituents of North Carolina ores.*

E. E. RANDOLPH, N. C. State.

*Photoelasticity and machine design* (Lantern). GASTON G. FORNES, N. C. State.

*The effect of an electric field on the viscosity of liquids.* A. A. DIXON, N. C. State.

*The vitamin G ( $B_2$ ) content of meals from certain oil seeds* (Lantern). F. W. SHERWOOD and J. O. HALVERSON, N. C. State.

\**The overwintering of urediniospores of Puccinia graminis tritici in North Carolina* (Lantern). ALBERT F. THIEL, W. C. of U. N. C.

*Physiology of Life in the desert* (Lantern). F. G. HALL, Duke.

*A new Phytophthora with spiny oogonia* (Lantern). Published in full in J. E. M. Sci. Soc. 54: 154-162. Leland Shanor, U. N. C.

- Factors in the ecology of East Greenland* (Lantern). H. J. OOSTING, Duke.
- x*The important rôle of salt spray in coastal ecology* (Lantern). B. W. WELLS and I. V. SHUNK, N. C. State.
- Fundamentals of glassine transparency* (Lantern). D. B. WICKER, N. C. State.
- xA *new form of tricolor mixer* (Lantern). CALVIN N. WARFIELD, W. C. of U. N. C.
- Notes on some higher fungi.* W. C. COKER, U. N. C.
- Relations of bottle characteristics to internal pressures in carbonated bottled beverages.* H. E. FULCHER and O. J. THIES, JR., Davidson.
- x *The relationship of acidity to the vitamin C content of the tomato* (Lantern). MARY YARBROUGH, MEREDITH, and G. HOWARD SATTERFIELD, N. C. State.
- Man versus animals.* C. S. BRIMLEY, N. C. State Museum.
- x*Genetic control of xenia in sweet corn.* H. S. PERRY, Duke.
- Ruffle-leaf of tobacco* (Lantern). S. G. LEHMAN, N. C. State.
- \**Advantages of North Carolina rainfall.* LEE A. DENSON, U. S. Weather Bureau, Raleigh.
- The structure of night* (Lantern). CHARLES M. HECK, N. C. State.
- x*Systematic jointing in sedimentary rocks* (Lantern). JOHN M. PARKER, N. C. State.
- Some observations upon the education of the scientist and upon the scientist as an educator.* J. P. GIVLER, W. C. of U. N. C.
- x*Triassic coals* (Lantern). WILLIARD BERRY, Duke.
- Peanut "pouts"* (Lantern). Z. P. METCALF, N. C. State.
- Direct gasoline injection for aircraft engines* (Lantern). L. R. PARKINSON, N. C. State.
- Riboflavin and a further growth essential in the tissues. Quantitative distribution and the influence of the food.* VICTORIA CARLSSON and HENRY CLAPP SHERMAN, W. C. of U. N. C.
- Geology of the Grand Coulee Dam, Washington* (Lantern). W. H. IRWIN, U. N. C.
- Disposal of sulphur black dye waste at the Davidson Cotton Mills.* O. J. THIES, JR., Davidson.
- x*Mineralogy of the Staley pyrophyllite deposit.* JASPER L. STUCKEY, N. C. State.
- †x*Climate of the Carolina highlands.* MARTHA E. NORBURN, Biltmore.
- Geomagnetic work in Franklin County, North Carolina.* H. W. STRALEY and W. RAY JOHNSON, U. N. C.

*Further studies on the origin of "Carolina Bays"* (Lantern). W. F. PROUTY, U. N. C.

*Mineralogy of desert sands.* W. A. WHITE, U. N. C.

*Schächenthal, a Swiss alpine valley.* FRANKLIN C. ERICKSON, U. N. C.

*The Kundt's tube experiment.* C. W. EDWARDS, Duke.

†*Host range studies with Bacterium solanacearum* E. F. S. (Lantern)  
T. E. SMITH, U. S. D. A., Oxford, N. C.

#### BOTANY SECTION

x*Bog levels* (Lantern). MURRAY F. BUELL, N. C. State.

*The growth of the cotton boll* (Lantern). THOMAS KERR, N. C. State.

*Environmental control of growth ring patterns in cotton hairs* (Lantern)  
DONALD B. ANDERSON, N. C. State.

*Plankton algae of North Carolina* (Lantern). L. A. WHITFORD, N. C. State.

x*Development and distribution of tobacco roots* (Lantern). L. J. GIER, Campbell College.

*Some unusual fungi.* FREDERICK A. WOLF, Duke.

*The relation between specific gravity of wood and its decay* (Lantern)  
KENNETH H. GARREN, Duke.

x*Some parasitic fungi harbored by peanut seed stock.* R. F. POOLE and M. M. EVANS, N. C. State.

x*The rôle of magnesium in chlorosis of peach.* J. CARLYLE HACKNEY, N. C. State.

x*Root resistance as a cause of decreased water absorption at low temperatures* (Lantern). PAUL J. KRAMER, Duke.

*Thornlessness in dewberry breeding.* CARLOS F. WILLIAMS, N. C. State.

*The occurrence of cellulose in the lower fungi* (Lantern). J. N. COUCH, U. N. C.

*Some problems in the distribution of certain mosses as evidenced by their study in North Carolina* (Opaque projector). LEWIS E. ANDERSON, Duke.

*The effect of light of various periods and wave-lengths on the growth and fruiting of Chōanephora cucurbitarum* (Berk. & Rav.) Thaxter (Lantern), GEORGE A. CHRISTENBERRY, U. N. C.

*Notes on Amelanchier.* H. R. TOTTEN, U. N. C.

x*The genus Euglena at Mountain Lake, Va.* (Opaque projector). DON RITCHIE, U. N. C.

*Grasses new to North Carolina* (Opaque projector). H. L. BLOMQUIST, Duke.

†*A remarkable fungoid alga*. W. C. COKER, U. N. C.

*Greenhouse experiments with certain copper and zinc preparations as seed treatment materials for cotton* (Lantern). S. G. LEHMAN, N. C. State.

x*Notes on a bacterial disease of the tubers of Jerusalem artichoke, Helianthus tuberosus*. LELAND SHANOR, U. N. C.

#### ZOOLOGY SECTION

*Relationships between primary and secondary sexual organs* (Lantern) RALPH BAUM and BERT CUNNINGHAM, Duke.

x*Life cycle of a sporozoan parasite of the oyster* (Lantern). HERBERT H. PRYTHERCH, U. S. Bureau of Fisheries, Beaufort.

*The dynamics of the human ossicles* (Lantern). OTTO STUHLMAN, JR., U. N. C.

x*Parasite* (Lantern). A. S. PEARSE, Duke.

x*Nutrition of certain wood-boring Coleoptera* (Lantern). HARVEY E. SAVELY, JR., Duke.

x*Polyclad larvae* (Lantern). GEORGE W. WHARTON, Duke.

*Hemoglobin in the Amphibia* (Lantern). F. H. MCCUTCHEON, N. C. State.

*Life history of the beetle, Passalus cornutus* Fab. (Lantern). I. E. GRAY, Duke.

#### MATHEMATICS SECTION

x*Some implications of Dupin's indicatrix*. J. W. LASLEY, JR., U. N. C.

*Removable singular points*. J. J. GERGEN, Duke.

*The matrix equation  $P(A, B, X) = O$* . H. M. NAHIKIAN, N. C. State.

#### PHYSICS SECTION

*A 600 kilovolt transformer unit for nuclear investigations*. J. C. MOUZON, Duke.

x*An apparatus for the study of weak absorption*. L. G. BONNER and H. SPONER, Duke.

*Wilson cloud chamber analysis of cosmic rays*. J. I. HOPKINS and W. M. NIELSEN, Duke.

*The infrared absorption of mixtures of polar and non-polar molecules*. GEORGE E. COUCH and E. K. PLYER, U. N. C.

*Composition of cosmic rays at sea level and under ground.* L. W. NORDHEIM, Duke.

*An analysis of a survey of the subject matter covered by twenty institutions in their physics laboratory courses for engineering students.* G. W. BARTLETT and CHARLES M. HECK, N. C. State.

*A new type of photometer.* J. B. DERIEUX, N. C. State.

*Certain recently observed physical phenomena in clouds.* CHARLES M. HECK, N. C. State.

#### EXHIBITS

*A method of cataloguing insects.* Z. P. METCALF, N. C. State.

*Growth rings in cotton hairs.* DONALD B. ANDERSON and THOMAS KERR, N. C. State.

*Tobacco ruffle-leaf.* S. G. LEHMAN, N. C. State.

*"Tulite viewer" (Lantern slides in three dimensions).* NEVILL ISBELL, Wake Forest.

*Composites of Wake County (150 species).* R. K. GODFREY and B. W. WELLS, N. C. State.

#### NORTH CAROLINA SECTION OF THE AMERICAN CHEMICAL SOCIETY

*The hydrolysis of human hair.* JAMES C. ANDREWS, U. N. C.

*Aqueous solubilities of some isomeric pentanols and hexanols.* P. M. GINNINGS, RHODA BAUM, and RUTH WEBB, Greensboro College.

*Certain condensations brought about by bases.* C. R. HAUSER and B. E. HUDSON, Jr., Duke.

*Activity studies in aqueous lead chloride solutions; an investigation concerning the Debye-Huckle ion-size parameter.* H. D. CROCKFORD and P. M. NICHOLS, U. N. C.

*Symptoms and growth response of rats on various degrees and types of vitamin G deficiency.* SUSAN GOWER SMITH, Duke.

*Some coloring matters derived from 2-5 dihydroxyacetophenone.* SAMUEL F. CLARK and ALFRED RUSSELL, U. N. C.

*The rate of reaction of chlorimines with sodium alcoholate; a contribution to the theory of rapid reactions.* WALTER JORDAN, State College, and DOUGLAS HILL, Duke.

*The vapor phase fluorination of organic compounds.* J. A. SOUTHERN and J. T. DOBBINS, U. N. C.

*6-halogenated carvacrylamines.* G. C. KYKER, U. N. C.

*Vitamin A in the liver of wild animals.* G. HOWARD SATTERFIELD and FRANCIS TRIPP, N. C. State.

*The synthesis of alkyl sulfonic acids.* R. W. BOST, Jr., P. H. LATIMER and J. K. HODGES, U. N. C.

*The decomposition of ammonium deuterium chloride.* E. C. MARKHAM and S. B. KNIGHT, U. N. C.

The following abstracts have been received:

*Hydraulic Separation of Mineral Constituents of North Carolina Ores.*  
E. E. RANDOLPH, State College.

Ores are often composed of non-homogeneous constituents, usually the valuable mineral constituents and the worthless or earthy material called gangue. The separation of the valuable material from the worthless material is called concentration and the valuable part is called concentrate. Often the concentrate contains in addition to the principal mineral constituent associated materials of economic value.

While it is true that a great variety of mineral matter is found in North Carolina, the percentage of valuable constituents in many of these ores is small. For a number of them special methods must be found to make it economically advisable to try to work them. Gold ore, for example, is widespread in the state. The assay value of many of these ores is low, and consequently only a few mines at present are in operation. From the fact that North Carolina has produced and shipped large quantities of feldspar the idea has been given that vast quantities still exist in the state, but we are informed that the available supply of easily obtainable No. I feldspar in the state is limited, so that new means should be devised of separating the No. I feldspar from lower grade material.

It has occurred to us that a combination of hydraulic settling, hindered settling, flocculation and deflocculation may make it possible to work certain low grade ores in this state. If we can recover associated materials which have a market in comparatively pure form, sufficient income may be derived from these associated products to make it profitable to operate.

The results of small scale laboratory work indicate that a combination of these processes will give satisfactory results. We are therefore engaged in constructing a pilot plant size equipment of sufficient capacity to obtain data for commercial consideration.

In the hindered settling produced by the upward air current in the water very finely divided particles are so intimately attached to the water particles that the apparent Specific Gravity is increased so that

two substances of very close Specific Gravities can be successfully separated.

In free hydraulic settling quartz for example with Specific Gravity of 2.65 does not satisfactorily separate from mica with Specific Gravity of 2.7 to 3.1 but with hindered settling they separate fairly well. The remaining suspended mixture can be separated by flocculation and deflocculation.

*The Important Rôle of Salt Spray in Coastal Ecology.* B. W. WELLS and I. V. SHUNK.

Observations made during the spring of 1937 prove that the repressed sloping form of the seaside shrubs ("wind forms" of the literature) is not due to wind but to the killing action of the salt spray in the wind on the young growing shoots.

Shrubs under observation were noted on April 30 to have suffered injury to the young shoots but this injury was confined to the southeast sides. At the Wilmington Weather Bureau Office 18 miles away we found a high wind had blown a week earlier for a period of 19 hours almost continually from the southeast, the weather at the time being overcast. The ground at this spring season was moist so that the possibility of the usual wind effect through bringing about excessive water loss was eliminated. The only other possible cause of the injury was that of the salt spray carried in the wind. Tests were made of the salt present on the surface of killed and unkilld shoots of similar size using silver nitrate solution—a strong precipitate being obtained in the case of the former and one almost undetectable in the case of the latter. An exposed shrub line extending across the peninsula and facing directly to the southeast gave perfect confirmatory evidence in that the further away from the sea the less noticeable was the injury, a fact which was to be significantly correlated with the progressive attainment of the normal rounded contour of the shrub form. Both sea water and sodium chloride of the approximate concentration of sea water, sprayed on uninjured shoots produced exactly the same pattern of injury as that produced by the salt spray.

It may be stated categorically that in the coastal region under observation that the spray factor is responsible for the "wind form" and not the wind factor. These coastal malformed woody plants should therefore be called "spray-forms."

Based upon transplants of *Aristida stricta* from an inland habitat to the front dunes and its death within a month's period, we suggest



that the species which are so distinctive of the ocean dune community are distinctive primarily because of their adaptation to the intense and omnipresent spray.

Our data thus point to a new and entirely unrecognized habitat factor; viz., salt spray—to be of primary importance in determining the composition and condition of all plants found in the wind created spray zone.

*A New Form of Tricolor Mixer.* CALVIN N. WARFIELD.

To demonstrate effectively the visual effect produced by mixing colored lights and by mixing colored pigments, the writer has designed and constructed a new form of tricolor mixer. An unique construction feature is the use of two wedge-type (i.e., small-angle) prisms to deviate two portions of the beam of light from a projection lantern so as to obtain three overlapping images on the projection screen. The use of these prisms immediately in front of the projection lens of the lantern results in an unusually compact and readily constructed color mixing device.

With this device one can perform quite readily all of the standard demonstrations of additive color mixing which are possible with the devices commercially available or described in the literature. Furthermore, by means of this device it is possible for the first time to demonstrate convincingly the relationship of the subtractive primary colors to the additive primary colors. To do so one has only to substitute a clear glass lantern slide with a solid circle of opaque paper mounted at its center, for a lantern slide consisting of an opaque card with a circular aperture at its center. The shadow of the opaque round card in the former gives rise to three overlapping circles of color which are the complements of the three produced by the aperture in the latter. Since the former circles of color are due to the absence of a certain color, their overlapping areas exhibit the subtractive effect, whereas the latter produce an additive effect.

*The Relationship of Acidity to the Vitamin C Content of the Tomato.*

MARY YARBROUGH and G. HOWARD SATTERFIELD.

A transverse slice was cut from the central portion of the tomato. The slice was quartered, two opposite quarters were used for the vitamin C determination and the other two quarters for the acid determination.

The method for the vitamin C determination was essentially that

of Bessey and King. A mixture of sulphuric acid and metaphosphoric acid was used for extraction.

The acid was determined by titration, using 0.1 N KOH with phenolphthalein as an indicator.

Thirty-seven comparisons were made. From the data obtained there seems to be no definite relationship between the acidity and the vitamin C content of the tomato.

*Genetic Control of Xenia in Sweet Corn.* H. S. PERRY.

The quality of sweet corn is commonly impaired by xenia resulting from natural cross pollination with starchy varieties grown in neighboring areas. An attempt to reduce this damage by introducing a gene which puts foreign pollen at a disadvantage is being made.

The gene *Ga* (chromosome 4) is being used for this purpose. In hand pollinations it is known that less than 5% of pollen tubes carrying the allele *ga*, for which common starchy varieties are homozygous, are successful in affecting fertilization in competition with *Ga* pollen tubes in silks of the genotype *GaGa* or *Gaga*.

By a series of four back crosses *Ga* has been converged upon Purdue 51, one of the parents of Golden Cross Bantam. Resulting hybrids possess the gene *Ga* and approach ("thirty-one thirty-seconds") a genetically pure strain of Purdue 51.

By substituting one of these hybrids for Purdue 51 it is hoped that a Golden Cross Bantam will be produced which will be practically unchanged except for a substantial reduction in incidence of xenia.

*Systematic Jointing in Sedimentary Rocks.* JOHN M. PARKER.

The clean-cut, plane joint fractures in the slightly deformed sedimentary rocks of central New York are grouped into two predominating sets intersecting at 80°, and lying nearly parallel and at right angles to the regional dip and the low folds. Changes in trend of the folds are accompanied by corresponding swings in the joint pattern. Some sets are double, the strikes showing two maxima averaging 19° apart. The restriction of dikes to the dip joints indicates contrasting open and closed types.

The position of these sets nearly parallel and at right angles to the fold axes (and hence to the compressive forces) rules out simple compressive shear breaks, as does the open and double character of some sets. Graphic analysis of the relative magnitudes of the normal and tangential components of a combination of tension and compression at right angles to each other, on shearing planes lying at various posi-

tions, indicates that fracturing will occur along planes making an angle of 10–20° with the direction of compression, because of the large *tensional* normal component here. A second position of shearing at angles of 65–75° is also expectable, but here with a *compressive* normal component.

These two possible positions of shearing, both approaching the stress directions, thus appears to account for the two principal joint sets. The double character of some sets results from conjugate fractures forming at each shear position, while open joints form where the normal component is tensional. Experimentally formed fractures confirm these conclusions.

#### *Triassic Coals.* WILLARD BERRY.

Triassic coals are found in Moore, Chatham, and Lee Counties in North Carolina. It is my intention eventually to work out a revision of the Triassic Flora of these coals and other Triassic areas in the state. However from a preliminary study on the coals themselves several new things have been discovered: First, that there are a very small number of spores in the coal and much woody tissue, and that the spores are as yet mostly all undescribed species and smaller than I would expect. And second, that there are some small fragments of glass in the coal. This glass seems to be volcanic in nature and would represent ash from contemporaneous volcanoes. It would also be older than the intruding diabase which has in places metamorphosed the coal. The coal bed examined in detail is the seam mined by the Deep River Coal Company near Gulf, Chatham County.

#### *Mineralogy of the Staley Pyrophyllite Deposit.* JASPER L. STUCKEY

North Carolina contains the only important commercial deposits of pyrophyllite ( $H_2Al_2Si_4O_{12}$ ) known in the United States. These deposits are found in Montgomery County near Troy, in Moore County near Hemp and Glendon, in Alamance County near Snow Camp, in Randolph County near Staley, in Orange County near Hillsboro, and in Granville County near Stem. The deposits in Moore County near Glendon and Hemp have been described in detail in Bulletin 37 of the North Carolina Department of Conservation and Development, "Pyrophyllite Deposits of North Carolina."

Developments at Staley have exposed a large body of pyrophyllite which contains minerals not observed in the deposits near Glendon and Hemp. A detailed study of the mineralogy of the deposit and the

relations of the minerals is being made. Minerals observed in the deposit which are related to the processes of pyrophyllite deposition are: quartz, pyrite, lazulite, topaz, kyanite, chloritoid, sericite, and pyrophyllite. The pyrophyllite and associated minerals appear to have been formed by the replacement of an acid volcanic fragmental rock mass through the agency of hot solutions of deep seated origin.

*Climate of the Carolina Highlands.* MARTHA ELIZABETH NORBURN.

The Carolina Plateau, located in the Virginia climatic belt (Koppen's Cfa), has the climate of a modified mountain complex in the temperate zone. However, the Plateau has its own distinctive features as indicated by the trend of the isotherms.

These characteristics are: (1) a temperature which is lower than the surrounding areas both in summer and in winter, the mean annual being 54.3°; (2) precipitation with great variation, the rainfall on the curve of the Blue Ridge which directly faces the rain-bearing winds, being the greatest in America except the Puget Sound Region and decreasing by zonal steps in accordance with the ranges. This rainfall has a spring and summer maximum of 14 inches, an autumn minimum of 9 inches, and a winter average of 13 inches; (3) lower relative humidity; (4) greater insolation; (5) greater variation in temperature due to difference in elevation and in direction of slopes; (8) greater wind velocity and variability in direction. The winds of autumn, winter and spring are controlled by the prevailing winds, whereas those of summer are the result of solar insolation and the resulting valley breezes.

Evanescient features of the landscape which are contingent upon climate are the extensive development of the radiation phenomenon of the thermal belt and its verdant zone, fog lines along the water courses in the summer and autumn, the magnificent cloud effects at all seasons, and the blue aerial haze which gives the region an ethereal aspect and forms one of its chief charms.

*Host Range Studies with *Bacterium solanacearum*.* T. E. SMITH.

A comparison has been made of the susceptibility of eighty-five plant species to *Bacterium solanacearum* by: (A) Natural infection when grown on naturally infested soil in the field; (B) Stem inoculations made with small wedges of woody tissue from diseased tobacco plants. All of the species positive to natural infection (27) were also positive to

stem inoculation but the opposite was not always true. Five species, cowpeas, soybeans, velvet beans, Lima beans, and *Canna* sp., were negative to natural infection but positive to stem inoculation. In detailed studies with cowpeas, soybeans, and velvet beans it was demonstrated that these legumes could be effectively used for at least one season in rotations for wilt control. Five other species, sweet potatoes, cotton, watermelon, fireweed, and *Crotalaria striata* have been included in one or more published host lists but in these tests were immune to both natural and artificial infection.

*Bog Levels.* MURRAY F. BUELL.

A series of levels run across a bog semiannually over a period of years revealed considerable fluctuations in the bog surface. The extent of this fluctuation in bog level varies from a small but appreciable change (about 4 inches) in mature bog forest underlain by about 10 meters of peat; to a foot and a half and more in marginal bog forest of tamarack below which the deposit is extremely deep. The sedge mat, which varied directly with the water surface showed a maximum fluctuation of 2.3 feet. The fluctuations over the deeper parts of the bog are sufficient to affect materially the results of peat profile studies and possibly sampling for pollen analyses.

*Development and Distribution of Tobacco Roots.* L. J. GIER.

A number of plants were removed from the beds by the soil block washing method and from the field by the trench method. Drawings and measurements were made of the root systems and the plants dried for shoot: root ratio studies. The ratio was found to be near 10:1 through the entire season with a consistently high correlation between the dry weights of shoots and roots. Mature plants were found to have about 1400 feet of roots. The experiments are being repeated this year under various conditions.

*Some Parasitic Fungi Harbored by Peanut Seed Stock.* M. M. EVANS and R. E. POOLE.

For the past several years, growers have experienced heavy losses in peanut plantings throughout the state. The diseases appeared to involve many causes, since there were heavy losses of juvenile plants, of older plants during the season, severance of nuts from the stem before harvest and decay of nuts. An examination of mature peanuts from the many localities of this state indicated that various lesions occurred on the outer coating of the nut as well as on the shell.

Many isolations were made from the infected parts. Among the large number of fungi isolated were well known and widely distributed ones including *Pythium ultimum*, *Sclerotium bataticola*, *Botrytis cinerea*, *Corticium vagum*, *Fusarium vasinfectum*, *Sclerotium rolfsii*, *Rhizopus nigricans*, and *Fusarium moniliforme*. There were apparently many species of *Fusarium* isolated, which are not yet identified. At least five distinct morphological strains of *Corticium vagum* were isolated. *Sclerotium bataticola* was obtained from all sources where samples were taken. Species of *Cephalothecium*, *Trichoderma*, *Penicillium*, and *Aspergillus* were also obtained.

Preliminary studies on plant inoculations have clearly shown that a very large number of the species of *Fusarium* isolated from the lesions on the nuts as well as the established parasites given above are parasitic on the peanut plant and its various parts under favorable conditions. It was revealed in these studies that *Sclerotium bataticola* attacks around 28°C. but not at 18°C. One strain of *Corticium vagum* attacked at 28°C. and higher only, while another strain attacked at about 18°C. and lower only. The other three strains seem to work in intermediate temperatures. *Botrytis cinerea* attacked at low temperatures. *Sclerotium rolfsii* was isolated from one source only, indicating that it may possess greater soil-borne than seed-borne activities. Some fungi caused discoloration and apparent injury to the roots without actually attacking the tissues.

These data thus far indicate very definitely that the peanut is a source of perpetuation and means of dissemination for fungi that are parasitic on most major and minor crops in North Carolina.

#### *The Role of Magnesium in a Chlorosis of Peach.* J. CARLYLE HACKNEY.

This is a report of research for a master's thesis done under the direction of Dr. R. F. Poole and Dr. A. J. Wilson.

The orchards in the sandhill section of North Carolina have for several years been damaged by a chlorosis which results in premature defoliation, decreased yield, and short life of trees.

In this work, a study was made of the relation of the magnesium content of leaves, twigs, and fruit of the peach tree to the occurrence of chlorosis; of the effect of application of magnesium compounds with the fertilizer on the magnesium content of the parts of the tree; and the effect of application of magnesium on the chlorosis.

Chemical analyses by the method of Josef Tischer (*Mikrochemie* 12: 65-86. 1932) showed that leaves from chlorotic trees had a lower

magnesium content than leaves from non-chlorotic trees. Application of magnesium as the sulfate or oxide increased the magnesium content of leaves, but not of the twigs or fruit.

Leaf-counts indicated that trees with no magnesium applied showed earlier defoliation than trees with magnesium applied.

*Root Resistance as a Cause of Decreased Water Absorption at Low Temperatures.* PAUL J. KRAMER.

The rate of movement of water through root systems of tomato and sunflower under a constant pressure over a temperature range from 0°C. to 40°C. was measured by decapitating the plants and attaching the stumps to a vacuum pump. It was found that the rate of movement of water decreased with decreasing temperature for both species, both for plants with roots in soil and in water. The rate of exudation from decapitated root systems not attached to a vacuum pump was negligible at 0°C., increased with temperature to about 25°C., and then decreased at higher temperatures. The rate of water movement through dead sunflower roots in water increased with temperature, but not as rapidly as it did in living roots. The slope of the curve for dead roots is approximately parallel to the curve for increasing viscosity of water, while the slope of the curves for living roots is considerably steeper. It is believed that the rate of absorption through dead roots is governed by the increasing viscosity of water as the temperature is lowered. In living roots the added effects of increased viscosity of the protoplasm and colloidal gels of the cell walls causes even more marked reduction in absorption of water at low temperatures. This increased resistance to water movement at low temperatures is equally effective whether absorption is brought about by the secretory phenomena causing root pressure or by the pull of the transpiration stream. It is believed to be the principal cause of decreased absorption of water at low temperatures.

*The Genus Euglena at Mountain Lake, Va.* DON RITCHIE.

About twenty species of *Euglena* have been reported from the United States. Thirteen have been collected in the environs of Mountain Lake, in Giles County, Virginia. As commonly occurs, the richest collections were made from places polluted by animals or human habitation, *E. deses* and *E. gracilis* frequently causing the water to appear green by reason of their numbers.

One unidentified species was found containing a red pigment, hae-

matochrome; and another, *E. acus*, regularly appeared without color. Two unidentified green species were collected, one with few chloroplasts and two large paramylum granules in each end; the other quite large ( $218\mu \times 20\mu$ ), containing a few scattered, rod-shaped paramylum granules.

The identified species were *E. deses* Ehrenb. (the commonest form at Mountain Lake), *E. tripteris* Dujardin (usually considered rare, but not so in this region), *E. limnophila* Lemm. (formerly considered a European species), *E. acus* Ehrenb. (colorless at Mountain Lake), *E. Oxyuris* Schmarda (present in atypical form), *E. spirogyra* Ehrenb., *E. spiroides* Lemm., *E. proxima* Dang. (previously known only from France and Columbus, O.), *E. variabilis* Klebs., and *E. gracilis* Klebs.

*Notes on a Bacterial Disease of the Tubers of the Jerusalem Artichoke, Helianthus tuberosus.* LELAND SHANOR.

Rot of the tubers of the Jerusalem Artichoke by the bacterium, *Bacillus carotovorus* Jones, is reported occurring in the field from two widely separated localities, one in South Carolina and the other in North Carolina. Infection in the field is found to be directly affected by the presence of considerable moisture. Varieties planted near the ditches in a terraced field showed more disease than did tubers of varieties planted back away from possible seepage from the ditches. The disease on tubers in the field is not as serious as the storage rot caused by this same organism.

Laboratory inoculations on tubers of ten different varieties showed a distinct difference in the susceptibility of the tissues of the different varieties to decay by this organism. After ten days incubation at room temperature, some varieties showed hardly a trace of rot while other varieties had more than half of the cut surface of the tuber decayed.

*Life-Cycle of a Sporozoan Parasite of the Oyster.* H. F. PRYTHERCH.

Since 1930 serious oyster mortalities, involving losses in excess of a million dollars, have occurred in five different coastal regions from Mobjack Bay, Virginia, to Lake Barre and vicinity in Louisiana. In each instance the oysters have shown an unusually weak condition of the adductor muscle and inability to maintain closure of the shell during dredging, transplanting, and shipping operations. Microscopical examination of weak and dying specimens from each region has disclosed a heavy concentration of spores in the tissues of the muscle, gills and



mantle, the number per oyster frequently amounting to several million. These resistant, thick-walled spores, ovoidal in form, are generally grouped in variable numbers (1 to 16) in hypertrophied host cells and surrounded by a crescent-shaped episore. The mature spore (length  $20\ \mu$ , diameter  $11\ \mu$ ) contains a single vermiform sporozoite folded twice on itself and is the resting or final developmental stage in the oyster.

The meats of dying infected oysters are readily devoured by the common mud crabs, *Panopeus herbsti* and *Eurypanopeus depressus*, in the intestine of which hatching of the spores takes place. The sporozoite escapes through a micropyle and develops rapidly in the crab into a large cephaline gregarine having a length of 220 to  $342\ \mu$ . The gregarines unite in pairs, migrate to the rectum of the crab where they become attached and form gametocysts. Rosettes of zygotes, or gymnosporos,  $4\ \mu$  in diameter, are released into the water with the rupture of the gametocysts and enter the oyster gill by means of a pseudopod. Here they are generally picked up by phagocytes and transported in the circulatory system to nearly all parts of the body. In the blood cells the zygotes develop into sporozoites which after becoming surrounded by heavy, double-walled sporocysts represent the characteristic resting stage found in *Ostrea virginica*. The possibilities of heavy oyster infections are great considering the general abundance of the crabs and their close association with the mollusc, and the fact that 40 to 86 gametocysts, containing from approximately 8,000 to 90,000 gymnosporos each, may be produced in a single crustacean host.

The life history and morphology of this sporozoan parasite resembles that of the *Porosporidae* described on the French coast by Leger and Duboscq (1925) and Pierre Hatt (1931). It is a heterogenetic gregarine with alternation of hosts, having the vegetative and reproductive phase in the intestine of decapod crustacea and sporogony in molluscs, particularly in lamellibranchs. The resistant, monozoic spores found in *Ostrea* are similar to those first described as *Nematopsis* by Schneider in 1892. The American form is a new species which will be named and described in detail in a forthcoming paper.

The effect of the parasite on adult oysters was studied by producing heavy infections in the laboratory. In bulk experiments with several hundred oysters, losses of 66 to 73 per cent were obtained over a period of 3 months. Kymograph records of shell movement of 35 heavily infected oysters showed abnormal and frequent contractions of the adductor muscle followed by loss of holding power and death of the molluscs. The injury to the oyster host may be due to a toxin given

off by the developing sporozoites or to actual physical obstruction of the circulation by the masses of enlarged, infected phagocytes found in the blood vessels of the gills and mantle.

Practical prevention of the destruction of oysters by this parasite is possible by control of the primary host, the mud crabs, and by exercising care in the selection of uninfected seed oysters for restocking growing areas. The crabs do not migrate and can be easily removed, before the beds are planted, by the use of dredges or scrapes equipped with fine mesh bags. In certain regions where valuable oyster beds have been abandoned or their productivity seriously reduced because of damage by this microscopic pest it should be possible to reestablish and increase production by the procedure suggested above.

*Parasite.* A. S. PEARSE.

As the terms parasite, commensal, and symbiont have been used very differently by botanists, phytopathologists, and zoologists the following usage, which seems to be most general, is proposed: *parasite*, a plant or animal intimately associated with another (host) organism and injuring it; *commensal*, an organism living with a host but neither injuring nor benefiting it; *symbiont*, an organism living with a host which it benefits and from which it receives benefit in return—mutualism. Because one who examines a host usually does not know whether other organisms found associated with it are beneficial, injurious, or indifferent, a general, non-committal term is needed which merely indicates that one animal is associated with another. For this the Latin word *consors* (*consortes*) is suggested.

*Nutrition of Certain Wood-boring Coleoptera.* HARVEY E. SAVELY, JR.

Twenty-two species of beetles were found that confine their feeding to the phloem of freshly cut pine logs in the Duke Forest. The larvae of *Callidium antennatum* Newm. (Cerambycidae) and *Chrysobothris* sp. (Buprestidae) burrow in the phloem of dry pine logs and score the sapwood to a depth of 1 to 3 mm. It was found that they feed only on the phloem. There was an abundant store of starch in the phloem of dry logs, and the phloem from freshly cut shortleaf pine contained 5 per cent starch (dry weight) in November. The larvae of *C. antennatum* do not secrete a cellulase nor do they contain symbiotic bacteria or protozoa in their gut. Both *C. antennatum* and *Chrysobothris* sp. remove starch from the phloem they eat. The area of the burrows made by larvae of both species were measured and the amount of

phloem that had been consumed was calculated. The dry weights of the larvae of both species were proportional to the weight of phloem they had consumed. The average amount of phloem consumed during the larval life of ten individuals of *C. antennatum* was in the ratio of  $77.9 \pm 3.1$  grams of dry phloem per gram of dry larva; for four larvae of *Chrysobothris* sp., it was  $79.0 \pm 3.1$  grams. Phloem-feeding insects as a class are probably able to subsist on the stores of starches, sugars, and proteins which are abundant in living phloem without digesting cellulose or depending on symbiotic bacteria or protozoa.

*Polyclad Larvae.* G. W. WHARTON.

The polyclads are at present divided into two main divisions: Acotylea, simple without suckers; Cotylea, complex with suckers. As has been pointed out by the students of trematodes and others, a thorough knowledge of life histories is important in the formation of a natural classification. The polyclads have three types of larvae, and it is therefore probable that there should be three main groups of the order Polycladida.

Four members of the Acotylea were found to have a direct development: *Stylochus inimicus* Palombi (1928), *Stylochus floridanus* Pearse (1938), *Stylochoplana floridana* Pearse (1938), and *Conjuguterus parvus* Pearse (1938). One acotylean had Goette's larva, *Eustylochus meridionalis* Pearse (1938). Three cotyleans had Müller's larvae: *Thysanozoon brocchii* Grube (1840), *Oligoclado floridanus* Pearse (1938), and *Prosthlostomum lobatum* Pearse (1938).

If we assume metamorphosis to be primitive in the polyclads, the genus *Eustylochus* with its simplified acotylean adult structure and primitive larva is most closely related to the hypothetical ancestral polyclad and should therefore be placed in a third basic division of the Polycladida. The other two groups can then be derived by assuming on the one hand a specialization of development to a direct type for the Acotylea and on the other hand a specialization of the adult anatomy for the Cotylea.

Further work on this problem is being done at Duke in hopes that more substantial support for this theory will be found.

*Some Implications of Dupin's Indicatrix.* J. W. LASLEY, JR.

At an ordinary point of a surface there exists an artificial representation of Euler's equation known as the Dupin indicatrix. It expresses the radius of normal curvature in any direction in terms of that in the

direction of the curvature lines and the angle which the direction in question makes with the direction which gives the maximum radius of normal curvature. If we make the curvature lines parametric, the expression for the tangent of this angle leads us to an ordinary linear differential equation associated with each diameter of the Dupin indicatrix. This differential equation provides us with a pencil of lines on our surface. In similar manner, to pairs of diameters of the indicatrix we have associated ordinary quadratic differential equations providing us with nets of lines on our surface. To involutions of diameters of the indicatrix we have associated bilinear differential equations furnishing us with involutions of lines on our surface. Two pairs of diameters determine an involution whose double lines are a unique pair separating harmonically each of the given pairs. This new pair may be regarded as the "product," in the sense of groups, of the two originally chosen pairs. There is thus implied on the surface a pair of lines given by a quadratic differential equation which is the "product" of the two quadratic differential equations giving the lines arising from the originally chosen two pairs of diameters. We may define an identity quadratic. This identity together with the quadratics giving the axes, the isotropics on the surface point, the asymptotes of the indicatrix, the characteristic diameters, and the diameters bisecting the axes form a closed commutative set in which inverses exist, but are not unique. We are thus led to a quasi-group. The implied nets of lines on the surface are respectively the identity, the lines of curvature, the minimal lines, the asymptotic lines, the characteristic lines, and the lines bisecting the lines of curvature. These lines and their implied involutions of lines are obtained in canonical form. A transformation of parameter leads to their general expression.

*An Apparatus for the Study of Weak Absorption.* L. G. BONNER and H. SPONER.

It is often desirable or even necessary to study absorption spectra at great absorption lengths. Finer details of a spectrum are better observed at lower pressures and long layers than at higher pressures and short layers, furthermore weak absorptions are preferably studied with long paths. Therefore an absorption tube 105 feet in length has been set up. The tube is constructed of stainless steel with inside mirror polish. The five sections of the tube are put together with special flanges. The tube is exhausted with a Hypervac pump and holds a vacuum of  $10^{-3}$  mm. for a period of at least one week. Light source

and lenses can be adjusted conveniently. Prism spectrographs and a 3 m. grating spectrograph in a portable Eagle mounting can be alternately used. The apparatus should prove of extreme use for the investigation of spectra in the photographic infrared where large absorption layers are usually required. Corresponding experiments have been planned. It will also be important for research in the ultraviolet, e.g. in a search for forbidden transitions. At present we are looking for such a transition in  $N_2O$  which should occur in the visible region and the existence of which is known so far only from a theoretical interpretation of the monomolecular decomposition of  $N_2O$ .

*A New Type of Photometer.* JOHN B. DERIEUX.

In the usual type of photometer, the standard lamp and the tested lamp are placed at the ends of a straight rail, and the photometer head is placed between the lamps, and moved along the rail for adjustment. In the new type, which I have designed, it is as if the usual rail were severed at the middle, and the two halves turned around the severed point until they make a right angle with each other, the lamps being at the free ends. The photometer head is mounted permanently, except for rotation, at vertex of the right angle formed by the two rails, or their point of intersection. Adjustments for readings are made by rotating the photometer head, with its screen, until there is equal illumination on the two sides of the screen, being produced in this type by the variation in the obliquity of the rays on the screen, or the change in the exposure of the two faces of the screen to the two lamps. The angular adjustment corresponding to a correct setting is indicated by a pointer attached to the photometer head, which plays over a quadrant degree scale placed between the rails.

Letting  $L_1$  and  $L_2$  represent the powers of the standard and tested lamps, respectively,  $d$ , the distance of each lamp from the screen, and  $I_1$  and  $I_2$ , the corresponding illuminations on the screen, we have, from Lambert's cosine law of illumination,  $I_2 = L_2 \cos a/d^2$  and  $I_1 = L_1 \cos (90 - a)/d^2$ , where  $a$  is the angle of incidence which the rays from the tested lamp make with the screen. When the illuminations are equal,  $L_2 \cos a = L_1 \sin a$ , whence  $L_2 = L_1 \tan a$ . (Due to this simple relation, I should like to propose the name "tangent photometer," as is used in the similar case of the tangent galvanometer.)

This new type has three advantages over the old one: first—if the lamps are not covered, the light from them does not fall upon the eye of the operator, since the lamps are behind him as he sits in the angle

between the rails and near the photometer head; second—if it is desirable to cover the lamps, a permanent rigid tunnel may be mounted along the rails and extending almost to the head of the photometer, leaving only the small space for it to rotate; third—the operator may remain seated, and not move along as in the usual type, and the degree scale in this new type may have a short radius and consequently short arc.

H. L. BLOMQUIST, *Secretary*.

# PROCEEDINGS OF THE ELISHA MITCHELL SCIENTIFIC SOCIETY

OCTOBER 19, 1937, TO MAY 17, 1938

378TH MEETING, OCTOBER 19, 1937

W. L. ENGELS: *Recent Trends in Comparative Vertebrate Anatomy.*  
J. E. MAGOFFIN: *Electrophoresis.*

Whenever two phases come into contact there generally arises a stratification of balanced electrical charges between the phases, one becoming positive and the other negative. Although several combinations are possible, the one usually encountered is that of a solid phase in contact with a liquid phase. If an electrical field is impressed across such a system, the negative phase tends to move toward the anode and the positive phase toward the cathode. When the solid surface is spread out over many small particles, these particles will move through the liquid when the external potential is applied. This is known as electrophoresis.

The speed of movement of the particles is dependent on the charge carried by the particles, the external potential, and the dielectric constant and viscosity of the liquid. This relation enables one to determine the charge of particles in colloidal suspension by measuring the speed of electrophoresis.

Several methods for measuring electrophoretic velocity were discussed, and the advantages, disadvantages, and difficulties involved in the use of each were taken up. A simplified cell for use with the ultra-microscopic, direct measurement method used by the author was described.

With this method, the effect of hydrogen ion concentration on the electrophoretic velocity of platinum, indigo, and sodium oleate sols was determined. From this data, and results of other investigators, it was concluded that:

- 1) Platinum particles in colloidal suspension, made by arcing platinum wires under water, owe their charge to the ionization of hexahydroplatinic acid, which is present in the surface of the particles.

- 2) Indigo particles acquire a negative charge by losing hydrogen ions from the imino groups in the molecule.

- 3) The micelles of sodium oleate sols consist largely of oleate anions.

## 379TH MEETING, NOVEMBER 23, 1937

A. G. BAYROFF: *The Experimental Social Behavior of Animals, I. The Effect of Early Isolation of White Rats as Measured by Two Periods of Free Choices.*

Two groups of rats of approximate genetic equality were separated from their mothers when nineteen days old. Those of one group were reared in isolation and those of the other were reared in groups. When approximately 115 days old each animal was offered one choice a day for sixty days between a compartment containing food alone and a compartment containing, in addition to food, two white rats. After a month's interval they were given another series of sixty daily choices, this time neither compartment containing food.

The results showed few cases of social preferences (going consistently to a compartment with rats), these being best observed in those rats that had been reared in solitude.

It thus appears that the nature of the early life is of itself no certain indication that the behavior resulting from that kind of a life will appear. Unless the present situation is an occasion for the occurrence of the behavior affected by the early life, it will not differentiate the normal animals from the special animals.

A. E. RUARK: *Atom-smashing Equipment.*

## 380TH MEETING, DECEMBER 14, 1937

J. A. WHEELER: *Basic Particles of Atomic Structure.*

Already in the days of Greek science a contrast developed between two points of view as to the structure of matter, a contrast which continues even to the present time in a division between a field theory of matter and a corpuscular theory of matter. In 470 B. C. Leukippos of Milet proposed a mechanical explanation of the world in terms of a vacuum in which were placed atoms without qualities which, however, were responsible in a secondary way for the qualities of material matter as we know it. In contrast to this corpuscular point of view, Empedokles of Akragas in 450 B. C. suggested that the changes of matter should be accounted for in terms of four perpetual elements, earth, air, fire, and water, under the influence of attraction and repulsion.

Detailed knowledge of the structure of matter came only when modern scientific methods had been developed. In four great years of scientific advance a deeper understanding was brought about. In 1895 W. K. Röntgen discovered X-rays and a controversy immediately



developed as to whether they were particles or waves. In 1896 Becquerel discovered radioactivity. In 1897 Thomson investigated the electron, and in 1898 the Curies obtained polonium. It soon became clear what was the criterion to distinguish between waves and particles. A charged particle is characterized by energy and momentum. It is deflected in an electric or a magnetic field. (An experiment was shown at this point demonstrating the deflection of electrons in a magnetic field.) Light and wave motion, on the other hand, are characterized by wave length and the property of interference. (The audience was shown a neon light and given the opportunity to examine the spectrum of this light with a grating of fine lines ruled on glass, demonstrating the interference of light.)

X-rays were found to show interference and were therefore classified as light. Electrons could be deflected and therefore were regarded as particles. More recent experiments have shown that there are links between waves and particles, pointing to the essential unity of the two ideas. First of all, electrons passing through sheets of matter where the atoms stand in regular array show the same interference properties as does light passing through a grating. Conversely, light waves passing through the gravitational field of stars show a deflection similar to the deflection experienced by material particles.

Secondly, not only are light waves and particles similar in regard to interference and deflectibility but light can be converted into matter. A beam of penetrating radiation of short wave length—gamma rays—is partially converted into positive and negative electrons, on passing through a thin sheet of lead. The newly found positive electrons created in the experiment are of short life. Almost instantaneously, after striking atoms in their path, these positive electrons combine with ordinary electrons, disappear, and the lost energy flies away in the form of radiation of the same nature as visible light but more penetrating owing to the shorter wave length.

The partial unification of ideas of particles and waves achieved by the above-mentioned experiments still leaves unanswered the rôle of the heavier particles encountered in a study of matter. So far no experiments have shown the possibility of creating or annihilating protons—the nuclei of hydrogen atoms—or the nuclei of other atoms. It appears that the high energies encountered in the study of cosmic rays may show effects which will give a better understanding of relation between the heavier building blocks of matter and the electrons and light waves which now fit into the picture presented by the modern quantum theory.

J. C. ANDREWS: *Mechanism of Acid-Base Control by Urine Excretion.*

One of the principal functions of urine excretion consists in the removal from the blood of the strong acids which are normal products of protein metabolism. The average diet results, in the normal individual, in the production of considerable quantities of two strong acids: sulfuric and phosphoric. The former results from metabolic oxidation of the sulfur present in varying amounts in all proteins and the latter from hydrolysis of phosphoric acid esters and conjugates in nucleo- and phospho-proteins. Other end products of protein metabolism (uric acid) and small amounts of unoxidized organic acids slightly increase the total amount of acid to be handled, while the burden is very materially increased when, as in the diabetic, acid products of incomplete fat metabolism must be handled.

To excrete such quantities of acid unneutralized would be biologically impossible because of the low pH involved. To neutralize them sufficiently with "fixed base" (sodium or potassium) would involve too great a drain on the body's supplies of these bases. The situation is met therefore by a combination of the two, aided by the production of ammonia from urea by the kidneys. Thus some acid is excreted unneutralized (thereby normally producing a urine more acid than blood) but the stronger acids are neutralized, to a large extent, by ammonia, thus minimizing the use of "fixed bases." The ammonia content is therefore higher, the more acid the urine and the number of equivalents of acid excreted as ammonium salts is normally always greater than the number of equivalents excreted unneutralized.

381ST MEETING, JANUARY 11, 1938

W. H. IRWIN: *The Grand Coulee Dam* (Illustrated).

382ND MEETING, FEBRUARY 8, 1938

A. RUSSELL: *The Chemical Structure of Some Natural Coloring Matters.*

O. STUHLMAN: *The Mechanism Called Nerve Conductance.*

383RD MEETING, MARCH 8, 1938

H. G. BAITY: *Some Factors Affecting the Decomposition of River Deposits.*

Z. P. METCALF: *The Making of Bibliographies.*

The purposes and functions of bibliographies were briefly discussed and the fact that they are essential in all scientific work was stressed. The author's present method of making a bibliography was discussed in some detail and the various methods used to index bibliographies was

described. The method of selecting papers in a bibliography was described and rules were given for including or excluding certain articles.

384TH MEETING, APRIL 12, 1938

C. C. JONES: *Visible Effects of Ionizing Particles*.

385TH MEETING, MAY 17, 1938

W. F. PROUTY: *Further Studies of the Carolina Bays* (Illustrated).

J. N. COUCH: *A Review of Work on Septobasidium* (Illustrated).

The following officers were elected for the year 1938-1939:

*President*—H. V. Wilson.

*Vice-President*—D. A. MacPherson.

*Recording Secretary*—Treasurer, J. E. Adams.

# TEN TWO-HEADED TROUTS FROM 32 MM. TO 203 MM. LONG —THE RECORD SIZE

By E. W. GUDGER

PLATES 17-19 AND 4 TEXT FIGURES

## INTRODUCTION

In 1929, I figured and described a fine two-headed brook trout from a privately owned fish hatchery in New York State. It measured 53 mm. (2.1 in.) from tip to tip and was 9 months old. It was the largest two-headed teleost on record at that time.

In November, 1934, Pathé News Inc. in one of its films showed pictures of some two-headed trout. The caption apparently located these fish at Pasadena, California. Through the courtesy of Mr. J. S. Connolly, General Manager, copies of these pictures were sent to me. These showed two small and one extraordinarily large two-headed trout. Now two-headed fishes are far from novelties in any fish hatchery. They occur by the hundreds, but, left to themselves, they almost all die at or before the final absorption of the yolk-sac. Or if they survive this ordeal, because of their deficient locomotive powers, they are apt to be persecuted by their fellows and to succumb to their injuries. Hence it was clear that this unusually large monster would be a great prize to a fish teratologist.

Satisfied that these fish were located somewhere in California (but not in Pasadena), I wrote letters to friends living in and to others who had recently travelled through California, and presently from two sources learned that there were unusually large two-headed trouts to be found in the Yosemite and in the Mount Shasta Fish Hatcheries. I forthwith got in touch with the officials of these hatcheries—Mr. Archie Thompson of the Yosemite, and Mr. E. V. Cassell of the Mt. Shasta Hatchery. From them I learned that each had large specimens (as such little fishes go) of two-headed trouts which were very much alive and were being cared for as pets. Hence it was necessary for me to wait until the fate common to such abnormal fishes should overtake these specimens before I could study them.

The two-headed trouts figured and described herein (excepting my

own 53-mm. fish) have been sent me by these gentlemen and from them I have been given full data as to the rearing to record-breaking sizes of these remarkable specimens. My best thanks are hereby gratefully tendered to Messrs. Cassell and Thompson for their kind helpfulness. Acknowledgment of help from others will be recorded when dealing with data so kindly sent in by them.

#### FIGURES AND DESCRIPTIONS OF SIX DOUBLE-HEADED TROUTS

These six trout will now be studied in the order of their sizes, and the history of each will be given when the specimen is described. In addition four fish, which have not come to me, but of which I have accounts, will be briefly described since they fill in in excellent fashion a gap in the procession of specimens which are before me. We will begin with the two smallest which came from the Yosemite Hatchery.

##### *No. I.—A 32-mm. (1.25-in.) Loch Leven Trout*

This little fish, from the Yosemite Hatchery, is the smallest of my series. Of its history little was noted save that both mouths fed freely. It was about three months old at its death but no cause for this was noted.

This small monster is very symmetrical, as Figs. 1A and 1B, pl. 17, show. Generally in two-headed fishes one head is better developed and is larger, or one head lies in and continues the main axis of the body, while the other is smaller and is generally set at an angle to the main axis. In fish No. I, the bifurcation is almost perfect, but careful study seems to show that in dorsal view the right head is slightly larger and longer (Fig. 1A, pl. 17). The left head is a trifle shorter and smaller and seems to swing slightly to the left of the median plane of the body. This is perhaps more apparent in ventral view (Fig. 1B, pl. 17). Possibly this almost bilateral symmetry is due to the youth of this little monster, and probably, had it lived longer and grown larger, disparity between the heads would have come about.

This specimen is only 32 mm. (1.25 in.) long "over all." The width between tips of snouts is 9 mm., between the inner eyes (hinder inner edges) is 2 mm. On the upper side the extreme length of the bifurcation is only 7 mm. There is but one inner pectoral fin. Whether it is the right or the left, with the other suppressed, I cannot say. It is single and it seems to arise in the tissues at the bottom of the fork and squarely in the center. In front of this fin and belonging to the inner side of the right head is the distorted left gill-cover of this head. It

has been pushed obliquely outward and forward. The inner eyes are normally developed and were undoubtedly functional. I am unable to find any trace of a lateral line on the inner side of either head. The forking is entirely too short for such to have developed.

The junction of the two heads on the upper surface takes the form of a large strong fold of tissue. Back of this is a Y-shaped groove, composed in front of a dorsal groove from each head. The two grooves are confluent behind into the single normal one which extends back to the adipose dorsal. In this groove is set the single anterior dorsal fin. All these structures are plainly visible in Fig. 1A, pl. 17, a dorsal view of this specimen.

The ventral surface, shown in Fig. 1B, pl. 17, is seemingly more complicated than the upper, but is really very simple to understand. In front between the heads is an isthmus or junction of ventral tissues. It is but 4 mm. back from a line joining the two snouts, hence its forward edge is 3 mm. forward of the similar dorsal yoke. To the left is seen the distorted inner gill-cover of the right head. Back of the isthmus is a Y-shaped groove, with short anterior wings and a long tail-groove which terminates at the anal fin. The outer pectoral of each head is present and seemingly normal. The paired pelvics are small and delicate but seem entirely normal.

From study of the external surfaces, one cannot say where the union of the anterior paired vertebral columns takes place. But in dorsal view, from the point of union of the two heads backwards, the body seems normal. On the lower surface, the normal surface area seems to begin at about the posterior base line of the pectoral fins. The fish is too young and its bony structure too lacking in calcium for it to be X-rayed.

*No. II.—A 45-mm. (1.8-in.) Eastern Brook Trout*

This fish (Figs. 2A and 2B, pl. 17), also from Yosemite Hatchery, is somewhat older and larger than the former—from which it is probable that both heads took part in feeding. It measures 45 mm. in total length, and hence is nearly 50 per cent larger than the former. It died at the age of about four months from an attack of water mold on the inner gills of the right head.

The distance between the centers of the snouts of the two heads is 19 mm.; that between the hinder lower edges of the inner orbits is 9 mm. The left inner eye seems normal, but the right inner eye is gone, probably destroyed by water mold—of which more later. The skin covering

the heads seems somewhat different from that covering the body. This is especially true of the left head. In what might be called the region of the nape of the neck, extending across from the top of one gill-cover to the other, is a faint line of demarcation (Fig. 2A, pl. 17). This, which is lacking on the right head, will be found very prominent in other and older fish.

The bifurcation, as seen both in dorsal view (Fig. 2A, pl. 17) and ventral aspect (Fig. 2B, pl. 17), extends relatively much further back than in fish No. I, and the forking is somewhat less symmetrical than in that specimen. The left head is rather closely in line with the axis of the body, the right head is somewhat deflected to the right. The fork has a long flat slope from the dorsal region to the ventral surface. It is marked off behind by a strong fold of tissue forming the two forward halves of a Y. Measured from a line joining the two heads, this fork is 17 mm. back. The inner and upper parts of the Y, in color, form, thickness and extent are more marked structures than the like in any of these two-headed fish. They are pad-like.

Both inner opercles are displaced forwardly and outwardly. No cause can be ascribed to that on the left head, but when the little fish came to me there was a large mass of water mold (now removed) protruding from the left gill-aperture of the right head. This was plainly the cause of the opercular distortion here. The left inner eye of the right head is gone, probably destroyed by the fungus, as are the gills of that side. Both inner pectorals are present. That of the left head is above, of the right below. They are about equally developed. When the little fish came to me the point of the pectoral on the right head extended into the gill-cavity of the left head. The fork being carried so far back, there is on the inner side of each short body a lateral line. These (faintly visible in Fig. 2A, pl. 17) unite at the base of the fork to outline a V.

On each side back of the curious thick pad-like yoke is a groove. These unite in the median line to form a single dorsal groove which grows shallower toward the second and single dorsal fin where it ends. There are two anterior dorsal fins, one on each side of the groove but united at the inner edges of their bases. This duplication would seem to indicate that the axial duplication extends behind this doubled fin.

On the lower surface, the situation seems simpler (Fig. 2B, pl. 17). The bifurcation is much shorter—9 mm. from a line (the "base line") joining the snouts back to the isthmus, 13 mm. to the junction of the belly folds. In front of the yoke, the two inner pectoral fins may be

seen. That of the right head is below the other and its point is directed into the inner gill-cavity of the left head. The outer pectoral of each head is present—the left one 11 mm. from the tip of snout, the right one possibly a shade further forward. Between the belly folds there is a Y-shaped groove extending back between the pelvic fins to the anus and anal fin. From this description and from Fig. 2B, pl. 17, it is clear that, whatever may be the vertebral formation, there is materially less external doubling below than above.

In specimen No. I, the right head seemed to be in the main axis of the body, the left head somewhat smaller and slightly off the main axis (Figs. 1A and 1B, pl. 17). In specimen No. II it seems that the left head is the predominant one and the right the secondary (Fig. 2A, pl. 17). The left head is longer and better developed—in part due perhaps to the growth of fungus in the inner gill-region of the right head. The left seems to continue the main axis of the body. This is even more apparent in ventral view (Fig. 2B, pl. 17). This condition is in accord with the general rule that one head is larger and better developed—the main head of the monster.

I was very anxious to obtain an X-ray photograph to show the vertebral structure of this monster. Efforts were made by two expert radiologists but the results were nil. It would seem that there was not enough calcium in the skeleton to cast the desired shadow.

### *No. III.—A 53-mm. (2.1-in.) Eastern Brook Trout*

This is the two-head previously referred to on which I published in 1929. Because it fits beautifully into the series, and that it may be compared with the other two-headed trouts, it will be redescribed here. The specimen I owe to Mr. A. A. Townsend, a private fish culturist at Yama Farms Brook Trout Hatchery, Napanoch, New York. Here is his history of what was in 1929 the largest two-headed teleostean fish on record. Mr. Townsend wrote in 1925 as follows:

This little two-headed brook trout was hatched in February, 1925, and died on November 2nd of the same year—9 months later. I kept it in a small box 2 feet long, 8 inches wide, and 9 inches high. I held the water at a depth of about 5 inches in the box with a flow of about a quart a minute going through it. The only diet of the little fish was fresh pig's liver ground through a  $\frac{1}{4}$ -inch plate of an Enterprise meat chopper five times. It died with a fungus growth on the gills. This was caused by the larger [left] head working the smaller head into the sand at feeding time. This was kept up until inflammation set in in the gills of the smaller head, then fungus came and killed it.



A glance at the fish in dorsal view (Fig. 3A, pl. 17) shows that the bifurcation extends further back than in the preceding fishes. The left head seems surely to continue the main axis of the body. The right head is smaller, shorter, and is twisted out of the vertical plane. The heads approach each other more closely than we find in either of the other fish and lie in almost parallel planes. The distance between the centers of the snouts is 9 mm. and the inner eyes are but 3.5 mm. apart. At the rear of the fork are two first dorsal fins, each on its own body. The bodies seem confluent just in front of a line joining the anterior bases of the dorsals. Beginning in the transverse plane of the hinder third of the dorsals is a marked groove extending back under and behind the second dorsals to end at the anterior base of the caudal. The two adipose dorsals arise each on its own body, but are *confluent at their tips*, a thing never before recorded so far as I know.

Let us now turn to a closer examination from above of the two heads (Fig. 3A, pl. 17). From the tip of the snout of the longer (left) head to the point of junction of the two bodies is 18 mm. The downward slope of the junction is much more abrupt than that found in specimen No. II. But close inspection of the fish shows, what is not brought out in the figure, that at about one-half the distance to the ventral surface there is a more gently sloping platform of tissue which extends forward to the hinder bases of the inner pectorals. Because of the crowded area in which these fins are found, they project upward and slightly backward closely appressed—the right above and the left below. Because the inner pectorals arise in the vertical plane of the gill-region, and because of their position, the inner gill-flaps of each head are curled sharply forward and outward. Some of the gills of the left inner side are visible.

Between the heads and the paired dorsal fins and extending down into the fork, there is some evidence of the peculiar pad-like structures seen on the preceding fish. At this time, even after these 13 years in preservative, these structures are fairly plain. Below in the fork on the inner side of each head there is a brief lateral line, but the heads are so close together and the inner pectorals are so crowded that these lines, placed deep in the fork and obscured by the inner pectorals, are not visible to ordinary sight. Across the nape of each head, but somewhat more marked in the right head, is a faint line as if there were a depression or constriction here between head and body.

On the ventral surface there is far less evidence of bifurcation and distortion (with one exception) than on the dorsal (Fig. 3A, pl. 17). The distance from the tip of the left head to the point of junction of the

bodies is only 12 mm. The outer pectoral fins seem to be placed about in their natural positions. Extending backwards from the point of junction of the heads is a mid-ventral groove. This reaches between the paired pelvis (which seem entirely natural) to the anus and to the single anal fin. The most abnormal structure on the lower side is the greatly displaced and outpushed hyoid region of the right head. This may in part be due to unequal contraction in preserving fluid, but it is pretty surely correlated with the fact stated by Mr. Townsend that the stronger left head dragged the weaker right one about in the sand in the feeding box, so that the hyoid region became abraded and hence was readily attacked and distorted by the water molds by which this little monster was brought to its death.

For an X-ray photograph of the skeleton of this monster and those of the other two-headed specimens to be shown later, I am indebted to the courtesy of my friend, Dr. Howard A. Kelly of Baltimore, and to the skill of his technician, Mr. E. A. Morrison. That of the 53-mm. fish (the one under consideration) is not so good as the others to follow, since the fish has been for many years in a mixture of formalin and alcohol and its skeleton has suffered. But considering the condition of the fish, Mr. Morrison has brought out the vertebral column surprisingly well (Fig. 4, pl. 17).

In looking at the little monster in external view (Fig. 3A, pl. 17), two things impress one. The first is that the left head seems surely to prolong the main axis of the body. The other is the sharp left bend of the trunk just behind the paired first dorsal fins. However, inspection of the shadowgraph (Fig. 4, pl. 17) shows a markedly different state of things. Looking from the tail forward, one sees the left bend in the vertebral column to be more abrupt than the external view has indicated. Forward of this the vertebrae are doubled and run parallel, one set for each head, for a distance of about 6 segments. There is one pair of very large vertebrae possibly composed of two fused segments. Forward of the doubling the left column makes a sharp left bend and straightens out to the left head. Unlike what is seen in external view, in the X-ray photograph forward of the bend in the body vertebrae, the vertebral column of the left head extends straight ahead and plainly continues the main axis of the vertebral column.

The conditions in external view and in the X-ray photograph expressly and unexpectedly contradict each other. For this difference I have no explanation, nor do I have any for the transverse bar seen in the X-ray picture (Fig. 4, pl. 17) just where the paired vertebral columns diverge.

The formalin preservative in which this monster had been for 12

years has so affected the skeleton that it is not easy to count the vertebrae. In the left trunk there seem to be about 24 vertebrae to the point of union, but numbers 23 and 24 seem ankylosed. The vertebrae of the right head and side are hard to count at the back of the head. Several are either fused or are overlapping so that in the X-ray photograph they appear as a solid mass. However, there seem to be about 23 from this point to and including the last of these individual vertebrae. Very confused is the picture where the two sets of vertebrae (about 6 in number) come to run side by side. Those of the left half (including the apparently doubled vertebra) seem larger than those of the right side. Perhaps the latter lie slightly underneath those of the left side. Then again it may be that those of the two sides are more or less fused. Had the shadowgraph been made when the fish first came to me, these points would surely be much clearer.

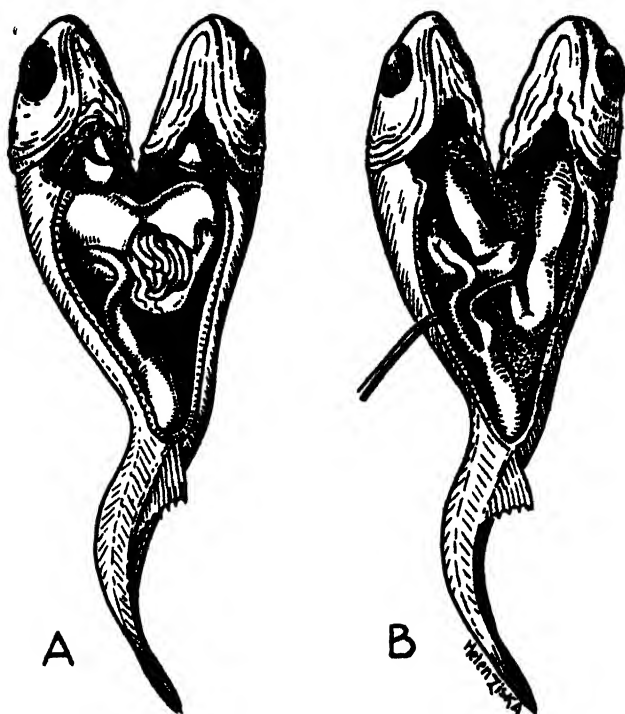
The single vertebrae—those of the tail—are about 27 in number. The number is not easy to make out, especially in the region of the bend and in that just forward of the caudal fin. None of these, not even the first (on which rest the right and left columns) seems to be enlarged.

We now come to a study of the internal structure of this monster, which has suffered much from the action of preservatives and from much handling in the 13 years since it came to me. Furthermore in the process of X-raying it, the external parts have undergone considerable disintegration—in a good cause. For these reasons the fish is no longer valuable for exhibition. So it was decided to dissect it to see what could be made of its internal structure.

When the ventral abdominal wall was removed, the viscera were seen as shown in Text-fig. 1A. In front is the heart of each head—the left one mutilated. At the junction of the two heads is the bilobed liver. The connecting part of the liver extends behind the junction of the two heads dorsad making a considerable bridge between the lobes. At the junction of the lobes, and particularly from above the left one, 8 or 9 pyloric caeca extend out. They lie ventrad to the oesophagus or stomach of the left head. On the right of the caeca is a part of the right alimentary tract, and at the rear of the abdominal cavity is another part of the canal ending in a large rectal section.

On removing the liver, the pyloric caeca, and other and unidentifiable tissues, the whole interesting alimentary canal system of the monster is to be seen as shown in Text-fig. 1B. In keeping with the fact that the left head is the predominant one, the left fork of the alimentary

tract is better developed (larger) than the right. It is impossible to say where oesophagus leaves off and stomach begins. In the central part of the body cavity, the stomach of the right head turns abruptly forward for about 5 mm. and then turns to the right and dorsad. At



TEXT FIG. 1. The abdominal cavity of the 53-mm. two-headed Brook Trout

In A, the abdominal wall and some of the gill-arches have been removed. Visible are the paired hearts, the tri-lobed liver, the pyloric caeca, and various parts of the alimentary tract.

In B, everything has been cleared away to show the paired anterior alimentary tracts and, behind, the single one formed by their union. As explained in the text, the parts of the canal have been somewhat displaced that they may be shown clearly in the drawing.

Specimen by courtesy Mr. E. V. Cassell.

this point the 9 pyloric caeca were given off. When the intestine reaches the dorsal wall of the body cavity, it makes another abrupt turn downward and then runs backward straight into the large intestine. The oesophagus-stomach of the smaller right head is some-

what smaller than that of the left head. It runs backward and then makes an abrupt turn forward. Next it twists around and runs caudad parallel with the ascending part. At the sharp twist is a small projection at which some very small pyloric caeca were given off. Then running backward it passes ventrad to the loop of the stomach and unites nearly at a right angle with the other intestine in front of the beginning of what appears to be a large intestine—certainly larger than both of its components taken together. The bends of the two alimentary canals are in several planes, particularly where the smaller right joins the larger left on its dorsal surface (Text-fig. 1b), hence it has been necessary to displace the parts and to draw the whole semi-diagrammatically—in one plane.

Externally the predominant head is plainly the left one. And internally it is equally clear that the left alimentary canal is the predominant one—the right, particularly in the hinder section, being subordinate.

*No. IV.—A 90-mm. (3.5-in.) Loch Leven Trout*

This specimen was presented by Mr. Archie Thompson, foreman of the Yosemite Hatchery. It was hatched about March 1, 1935. Mr. Thompson writes that it had no especial care apart from the other fingerlings. It was fed on a straight liver diet. Both heads ate and in general it acted as did the normal fish. It died of a fungus infection of the gills about February 15, 1936, at the age of about 12 months. It measures 90 mm. (3.5 in.) in total length and is the largest two-headed teleost thus far recorded. The fish was in weak preservative when it came to me and when the measurements (noted herein) were made. Immersion in stronger alcohol in the months since has produced some slight shrinkage.

In dorsal view (Fig. 5A, pl. 18), it may be seen that this specimen is unsymmetrically bifurcated. The left head is the main one, is longer and better developed and more nearly continues the main axis of the body. Furthermore, the right head is twisted and flattened somewhat. The distance between the points of the snouts is 37 mm. and between the inner eyes at their closest points is 15 mm. The inner eyes seem entirely normal.

From the tip of the snout of the left head to the point of union of the bodies is 31 mm., from the tip of the snout of the right head to the same spot is 25 mm. The first and second dorsals are single and normal. Just in front of the anterior base of the first dorsal is a marked concavity. The inner pectoral of the right head is poorly developed

(very slender) and extends upward and slightly forward over the hinder gill-region of the inner side of the left head. The inside opercle of this left head is bent sharply forward and is badly distorted. The left gill-region of the right head was overgrown with a great mass of fungus. Most of this has been pulled off in order to show the adjacent parts.

The right (inner) pectoral of the left head is somewhat overdeveloped, but it extends in the normal position (see Fig. 5A, pl. 18) under the left jaw of the right head. The short lateral line on the inside of the left head is not visible in Fig. 5A, pl. 18. The tissues on the inner side of the right head have been so affected by the fungus that only the hinder moiety of the lateral line is visible.

An interesting thing—and one for which I have no explanation—is that each head on the upper side, back to the nape-of-the-neck region, is covered with a curious skin as shown in Fig. 5A, pl. 18. This on each head is sharply delimited from the skin of the body proper by a faint groove reaching across the back of each head from the free edge of one upper gill-cover to the other. For the beginnings of this let the reader turn to Figs. 2A and 3A, pl. 17. This curious and abnormal head-covering reminds one of the "corselet" found on the head and shoulder region of some of the tunnies. The outer gill-cover of each head has some of the pigment spots found on the body of the fish, but the region between and behind the inner eyes is totally devoid of these. On the upper surface of each head, neither scales nor chromatophores are visible, though both are plain back of the transverse line.

The ventral surface (Fig. 5B, pl. 18) in first view plainly shows that the left head is the predominant one and more in line with the main axis of the body. The point of union of the heads is but 26 mm. from the tip of snout of left head, and only 22 mm. from tip of snout of right head. The paired pelvics and the single anal are entirely normal. Not so, however, the outer pectorals. That of the left head seems to be normal, and strange to say the inner pectoral of this head seems to be displaced forward by only about half the width of its base. The outer pectoral of the right head is, however, displaced backward, in consonance with the subordinate size and position of the right head. Plain also is the disturbance and destruction of the inner gill-parts of this right head by the growth of fungus (removed by me as noted above).

Studying this little monster as best one can externally, one concludes that the junction of the anterior paired vertebral columns must be effected under or slightly behind the single dorsal fin.

At first glance at Fig. 6, pl. 18, it is seen that this monster was in

first class condition for X-ray photography and that Mr. Morrison has done a splendid job. The shadowgraph here confirms the conclusion formed from external study that the left head is the main one, the right the secondary one. Here also the excellent portrayal of the lateral processes and the ribs gives an additional check on the count of vertebrae. Thus in the left anterior vertebrae the first three seem confluent, but these additional factors keep the count straight. However, the twisted position of the right trunk has made somewhat difficult the count of the segments on this side.

On the left side there are about 21 or 22 vertebrae (counting as 3 the anterior coalesced one). The count at the rear is very difficult. On the right one can make out 16+ vertebrae fairly clearly until they become obscure, but about 25 ribs can be counted to the beginning of the bifurcation. Just behind the fork there is a confused mass of osteological material in which there are possibly 6 or 7 vertebrae involved. These seem to be coalesced right and left vertebrae or unusually large normal ones, very much crowded. Back of these there are about 20 tail vertebrae.

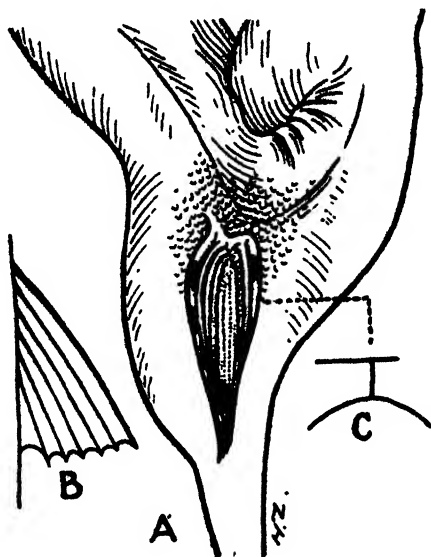
*No. V.—A 115-mm. (4.5-in.) Eastern Brook Trout*

Superintendent E. V. Cassell of the Mt. Shasta, California, hatchery has kindly sent me this specimen, which was raised by Mr. Elwin C. Anderson (fish culturist in the hatchery) who, as will be seen later, has had the most extraordinary success in rearing these trout monsters. Unfortunately, this specimen was put without wrapping in a jar with another abnormal fish (of another kind) and became jammed and distorted by the pressure of the larger fish. It is so twisted that I cannot have made either ordinary or X-ray photographs. However, I shall be able to describe the monster and give some measurements.

This two-head is just about 5 years old. Straightened out it measures about 115 mm. (4.5 in). The left head, which is normally twisted to the left, is the larger and dominant one, continuing the main axis of the body. From the tip of its snout to the point of junction is 44 mm. The same measurement for the subordinate right and smaller head is about 14 mm.—the twisting of this head makes more exact measurement impossible. The left head has normal eyes. The right head was born blind. The inner pectoral fins have their bases about 3 mm. apart. That of the right head stands nearly vertically. That of the left head arises in front of the other and extends up under the other. Both fins despite the crowding are normally developed. Due

to the crumpling of the right head in transit, little can be said about the fork or the conditions in it. Barring the fact that no trace of a lateral line can be made out on the inside of either head, the structures in the fork seem quite natural.

The first (or anterior) dorsal fin possesses such an extraordinary make-up as to call for figures and description. It stands just back of



TEXT FIG. 2. The abnormal dorsal fin of the 115-mm. monstrous Brook Trout

In A, the flattened fin (in dorsal aspect) is seen just behind the junction of the two heads.

B is a lateral view of the erected fin. The heavy line above represents the flat surface of the fin seen in A. The horizontal line represents the dorsal surface of the fish. The five rays of the unpaired hinder part of the dorsal are shown erected to tilt forward the flat part of the fin.

C is a diagram (in the dotted line across the fin) to show that the vertical part of the fin is to the right of the center of the flat part.

Specimen by courtesy Mr. E. V. Cassell.

the central edge of the declivity into the fork (Text-fig. 2A). As seen in this figure it is single but is confluent of two fins, one from each side. The anterior base (showing its double origin) is bluntly forked like a V with a short tongue of normal skin extending between the arms of each base. The confluent fin (20 mm. long backward from base to



tip) is flat on top (Text-fig. 2c). This flattened dorsal fin shows in its structure the relative dominance of the left head. The left part has three strong rays plus an inner weak one, the right but two strong rays and a weak one—hence the left side is the major one. Between these outer rays, the central tissue shows striations but no rays. Further, as shown in Text-fig. 2b, underneath this flat surface is a central fin in which are found the missing rays. The base of this central vertical portion of the fin extends backward about half the length of the fin. These five rays in life were undoubtedly capable of erection, thus lifting the flat surface and tilting it forward. This structure and action are shown in the cross-sectional diagrammatic Fig. 2c. As shown, the basal portion of the fin is placed excentrically—i.e., to the right of the center of the striated part of the flat fin of whose missing rays the vertical part is composed. Here again is seen the dominancy of the left side.

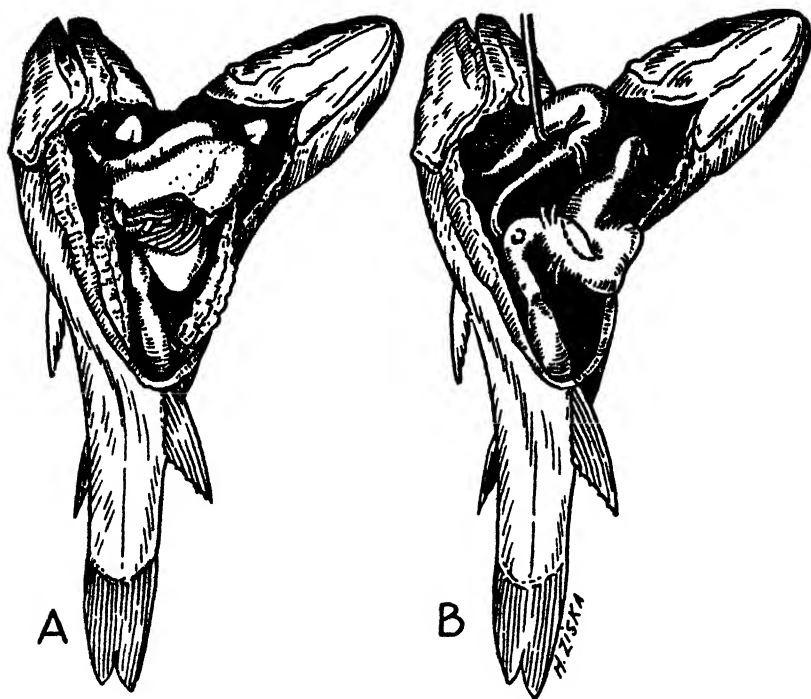
No such abnormal dorsal fin, as that shown in Text-figs. 2A, B, and C and noted herein, has ever before been figured and described. It is double and horizontal above; single, vertical and normal below. It is indeed a "*lusus naturae*" of a unique kind.

The second dorsal is normal. Behind the first dorsal fin there is a bad hump in the body upward and to the left. At this point the tail is twisted out of the vertical plane and to the right. Mr. Cassell notes that these conditions were present in life.

Due to the pressure-deformation of the right head, it is hard to know just how the ventral surface appeared normally. It is plain that the two heads were far apart. The shelf connecting them is large and projects forward greatly—having the two inner pectorals seated on the upper surface. The outer pectoral fin of the left head is normal in place but is only about one-third the size of its fellow in the fork. The outer pectoral of the right head is reduced to about the same width as that just described but is only about one-third as long. The base of the right pelvic is displaced forward about 4 mm. and the fin is somewhat smaller than the left pelvic.

From this description it is plain that the right head was subordinate to the left from the time when it was hatched blind. It could feed if the food was placed close to the mouth. As noted, all the right side organs are more or less deformed. The hump, raised up and pushed to the left, in the back in the level of the hinder dorsal, plainly indicates some great crumpling in the spinal column. It is evident that, even had this fish not been distorted in transit, it is the most abnormal of this series—particularly on the right side.

It is greatly to be regretted that ordinary and X-ray photographs cannot be made of this specimen. Furthermore, the distorted monster is not available for exhibition. But, under these circumstances it seems well to dissect it for the internal structure, which one would expect *a priori* to be as abnormal as is the external morphology.



TEXT FIG. 3. Visceral anatomy of a 115-mm. two-headed Eastern Brook Trout

In A, are seen hearts, liver, caeca, reproductive organs, and parts of the alimentary tract.

In B, are shown the parts of the digestive canal, doubled in front.

Specimen by courtesy Mr. E. V. Cassell.

When the ventral body wall is removed, things are found as shown in Text-fig. 3A. In front in the throat region of each head is found the heart. In the rear on each side is a well-developed reproductive organ (sex not determined). Across the front immediately behind the junction of the two heads on the ventral surface is the large stomach of the right head extending clear across the coelomic cavity to the point where

one would expect to find the stomach-oesophagus from the left head. Behind this organ is the large liver, not bilobed but having a crease running in the axis of the left head. Projecting from and dorsad to the left side of this large liver are about 11 pyloric caeca. Above on each side and behind these caeca are parts of the left alimentary canal.

Removing the sex glands, the liver with the gall bladder on its dorsal surface, and the caeca, we have left only the alimentary system. The oesophagus-stomach of the right head runs to the left as seen in Text-fig. 3B, and then bends abruptly down and runs to the right. At about half the way over, the stomach gives over into the duodenum. At this point, 4 small caeca are found. The gullet-stomach of the left head runs backward above the liver and the stomach of the right side, and as Text-fig. 3B shows is much twisted. At the point where the stomach goes over into the duodenum, the caeca are found (four stumps only shown). Beyond these the duodenum makes a bend of about  $180^{\circ}$  and as a rectum-like organ runs straight back to the anus. The duodenum of the right head bends around and runs to the right, and joins almost at a right angle with the duodenum from the left head to form the rectum-like organ. As in the case of the other fish dissected (Text-fig. 2B), the duodenum from the smaller head enters the main straight away intestine on its dorsal side.

It is plain that this doubled alimentary tract is much crowded and hence very much twisted. In order to make things clear to the reader, the folds have had to be somewhat displaced and drawn semi-diagrammatically to show the parts clearly. It is surprising to find that part of the tract belonging to the smaller and subsidiary head is so well developed even though smaller than that of the left or main head. Comparison should be made here with the like make-up of the doubled alimentary canal of the 53-mm. fish (Text-fig. 2B).

#### Four Large Two-headed Trout Described But Not Seen

Information has come concerning four two-headed trout intermediate in size between that last described and the giant whose study will bring this paper to a close. Two of these fishes were alive on last accounts, the other two have long been gone; but although none is available for study, yet to complete this series it may be well to describe them briefly from the data sent in to me. They bridge over the gap between specimens at hand of 115 mm. and 203 mm.

### Two At Tahoe Hatchery, California

Lengths about 110 mm. (4.3 in.) and 120 mm. (4.7 in.)

A chance newspaper clipping about abnormal young trout in the Tahoe Hatchery led to my getting in touch about a year ago with Superintendent J. C. Lewis, who has kindly supplied information concerning two two-headed trout of the sizes noted above. Their extraordinary development has been due to the personal care and attention given them by Mr. F. E. Setley, one of the hatchery men. The trout were alive when Mr. Lewis wrote me last.

The 110-mm. fish measured 30 mm. between tips of snouts, and 30 mm. from the tip of a snout to the point of junction of the two bodies. The 120-mm. fishlet also measured 30 mm. between points of snouts, but from snouts to point of junction of heads only 10 mm. The first fish has heads set on fairly widely forked bodies, the second has the heads almost confluent in the gill-region. These measurements are of course more or less approximate, since the fish were alive and could be handled but little.

These fishes are now four years old and that the reader may understand why they are so small for their age—compared with those described above—he must be told that they have spent their lives in water having a constant temperature of 40°F. This all the more emphasizes the excellent “job” done in keeping these monsters alive for four years.

Mr. Lewis describes an interesting habit of one of these fish. It swims about very little but always upside down (dorsal fin below). And it even rests on the bottom (where it spends most of its time) dorsal side down. Now certain fishes of the African rivers and lakes normally swim belly up, but in the case of this trout, there must be some air bladder defect.

### Two Formerly at Yama Farms Hatchery, New York

In 1929, Mr. Townsend (referred to above) wrote me of two two-headed trout larger than the one (Fish No. III above) he had sent me. These were isolated and fed carefully and copiously and as a result grew to a size larger than that figured and described in 1929. The intent was to see to what size they could be reared.

No. 1, the smaller, grew to about 127 mm. (5 in.) before fate overtook it. It was kept in a box on the floor of the hatchery. One day the cover was left off the box and a cat did the rest. It was then about

11 months old. It is a great pity that it could not have been carried further in development.

No. 2 attained a length of about 130 mm. (5.1 in.) before it too was lost. Mr. Townsend writes that:

The other little two-headed trout lived 11 months and grew to be 5½ inches long [130 mm.]. It was kept separate in a box as was the one I sent you, and when it grew pretty large was transferred to a larger box. While I was away for a few days, a heavy thunderstorm came up and flooded everything and, as the attendant forgot about it, the box and fish were washed away. One head was larger than the other and in feeding it dragged the other about on the bottom. This is the great difficulty in rearing two-headed fish. Whenever one head of the 5½ inch fish got sore by reason of the other head rubbing it on the bottom, I would take the fish out and put a mild solution of peroxide or of iodine over the head and body at the same time protecting the eyes. This would always stop the growth of fungus. It was a perfectly healthy fish and if I could have kept it, I am sure that I could have raised it to be a large trout.

Having studied the smaller fish in ascending order, we are now ready to take up the study of the largest two-headed fish of which there is record. This is the one shown in the Pathé News, the early figures of which started me on this study.

*No. VI.—A 203-mm. (8-in.) Brown Trout*

This fish is literally a "monster," huge, gross, and misshapen—as may be seen in Fig. 7, pl. 18; and Figs. 8 and 9, pl. 19. It is humped high in the dorsal region, and in packing and furthermore in shipping its tail has been bent downward and to the right. It is the oldest and largest two-headed teleostean fish on record. There are on record two-headed young elasmobranch fishes 9 to 12 inches in length. But these viviparous young sharks have been nourished in the uterus of the mother, and when captured free in the water are probably but a few days or at most weeks old. This two-headed trout at its demise was 7 years and 7 months old.

The story of how this fish came finally to me may not be devoid of interest. Antedating the Pathé News film, it goes back to July, 1933, when hearing that there was a large two-headed trout at the Mt. Shasta Hatchery, I wrote for information about it. Superintendent E. V. Cassell answered that he had such a fish, 4 years and 4 months old and in fine condition. Furthermore he kindly sent me a picture of the fish which, if taken in natural size, indicated a fish about 4.5

in. long. I then asked for it on its demise for study. Later came the episode of the Pathé News picture, which I believed to be of this fish—as indeed it turned out to be. Thereupon I wrote again in October, 1936, and was told that the fish had died and had been sent to Prof. J. O. Snyder of Stanford University. I tried to get Dr. Snyder to describe this monster in connection with the specimens from the Yosemite Hatchery above noted, but with great generosity he declined, sent me the fish and urged that I undertake the task.

For the personal history of this extraordinary specimen, I am indebted to Mr. Elvin C. Anderson of the hatchery crew. Mr. Anderson brought the fish up “by hand” making a pet of it under the name “Cuthbert.” Perhaps I cannot do better than quote Mr. Anderson’s letter.

I picked this fellow out of a hatchery trough of young German brown trout and put him by himself in a box with a screen above and below him. The box was about 40 in. long and 16 wide and about 6 gallons of water a minute flowed through it.

I kept him this way about two years. But so many people wanted to pick him up or make him swim, that I put him in a box about 32 in. long with a glass over it.

When he was about five years old, I found that in swimming slowly he did not clear the bottom and that in sliding over the slightly rough bottom he was developing a sore on the left side of the belly back of the head. To prevent this I put a sheet of glass at the bottom of the box.

In the spawning season of 1935, while I was away taking eggs, there was a general overhauling of the hatchery troughs and Cuthbert was put in a box with about 100 other young fish. This trough was 16 feet long and had a flow of about 15 gallons of water per minute. After about two weeks, he died without any particular cause that we could find. I gave this fellow all that he could eat with both mouths all the time. He lived to be 7 years and 7 months old.

And Mr. Anderson by his patient care of this fish has made the world’s record, for this is the largest and oldest two-headed bony fish ever figured and described.<sup>1</sup>

<sup>1</sup> Mr. G. P. Whitley, in the Australian Museum Magazine for February 20, 1937, has an interesting article, “Double-headed Fishes in Australia and New Zealand.” In this he refers to an article by J. G. Hay, “Something about Fishes,” published in West Australia in 1909. In this is a figure (copied by Whitley) of a two-headed snapper (*Chrysophrys auratus*) taken off Auckland, N. Z. It is figured as having two heads and shoulders, one body and tail, and is said to have weighed 28 lbs. Hay says that it was in the Auckland Museum, but neither fish nor record can be found. Whitley queries that “Perhaps it was a fake.” This is my judgment also. So rare a specimen would surely have been recorded and preserved.

Unfortunately no measurements were made of the just dead fish. These must be made now after the fish has been in preservative for about three years, and has undoubtedly undergone some shrinkage. Furthermore the measure of its length is made somewhat difficult by the double twist in the tail (Figs. 7, pl. 18, and 9, pl. 19). But straightening out the fish as well as possible, I find a fair "over all" measurement at this time to be about 203 mm. (8 in.). Its girth at the front base of the dorsal is 178 mm. (7 in.), and its weight is 226.8 g. (8 oz.). It measures 70 mm. between the points of the snouts and 22 mm. between the hinder edges of the eyes. The distance from the central line of the fork to the point of the left jaw is 55 mm., to the point of the jaw of the right head is 58 mm. These measurements cannot be checked on Fig. 7, pl. 18, owing to foreshortening in the photograph.

As Fig. 7, pl. 18, shows, the fork arises immediately behind the gill-covers. The left head plainly is the head of the fish despite the fact that it is twisted to the left out of the vertical plane of the body and is slightly shorter than the other. The right one is set at about an angle of 45° to the main axis of the body but it is nearly in the vertical plane of the body. At the center of the fork, the descent toward the ventral surface is beyond the vertical—there is a slight overhang. The inner gill-covers, because of the small space between the heads, are greatly distorted. That of the left head is greatly thickened and the edge is rolled inward and projects upward at the upper hinder edge as a double thumb-like object (Fig. 7, pl. 18). The inner gill-cover of the right head is rolled upward and inward, and is much distorted at the bottom. That of the left head shows clearly in Fig. 7, pl. 18, but that of the right head is far down and almost entirely concealed by the left pectoral of the right head. A thumb-like portion may be seen to the right of the vertical right pectoral.

The inner pectorals are greatly displaced owing to the crowding of organs between the heads. Their bases are coterminous—they are almost fused. The fin of the left head is more nearly in its natural position but it extends forward and outward below the right head pectoral, and gill-cover (Figs. 8 and 9, pl. 19). The right head's inner pectoral is better developed so far as size is concerned but it points nearly straight forward between the heads (Figs. 8 and 9, pl. 19). It certainly could not be used, and one may doubt any use of that of the left head (Figs. 8 and 9, pl. 19). The relative positions of the inside organs of each head are well shown in a head-on view (Fig. 8, pl. 19). There is no evidence of any lateral line in this very short fork.

In this head-on aspect (Fig. 8), the bulldog-like appearance of the heads and mouths is very apparent, as is the great crowding of the inner pectorals. The right head, as the somewhat subordinate one, shows more distortion than the left or predominant head. Its lower jaw is twisted to the left (Fig. 8, pl. 19). The right maxillary of the left head seems normal but is enlarged, the corresponding organ on the inside of the right head has the hinder part curled upward and then forward very much like a fish-hook closed up on itself (Fig. 8). This might be attributed to the proximity to the distorted gill-cover save that the two organs are here 5 mm. apart. The outer maxillaries of each head are invisible, but that of the left head is upturned at its hinder end to form the beginning of a hook—but one very thin and flat. The outer maxillary of the right head is curled upward and forward in a larger hook than that on the inner side—the point being covered over by a thick fold of tissue just below the eye.

In this same front view (Fig. 8, pl. 19), the bulldog-like appearance of the heads and mouths is very marked. This is somewhat apparent in the front view of the heads of the 90-mm. fish (No. IV), but in our present specimen there is an appearance of ferocity in each mouth. Noticeable in each jaw are the segmental gum-structures. These are made up of soft tissue, and in the back of each is a sharp backwardly recurved tooth. While present, these gum-like organs are less developed in the upper jaws, but each segment has its tooth at the rear.

The eyes and nostrils on each side of each head are normally developed. The heads are set low (Fig. 8) in relation to the high humped body back of them. The point of junction of the two heads is in the light seam-like line running back toward the depression in front of the dorsal fin. Plainly seen in Fig. 8 are the huge gill-cover of the left inner head and the rolled up thumb-like piece behind it.

Seen in frontal view (Fig. 8), but much more apparent in dorsal view (Fig. 7, pl. 18), are curious encircling lines in the neck region delimiting each head from the body. The beginnings of these lines were noted faintly in the 45-mm. fish (Fig. 2B, pl. 17). They were somewhat more apparent in the 53-mm. monster (Fig. 3A, pl. 17), and were very plain in the 90-mm. trout (Fig. 5A, pl. 18).

On the "neck" of the inner side of the left head of this largest (203 mm.) fish, there is a strong beginning of this just behind the upthrust finger-like fold of the edge of the operculum (Fig. 7, pl. 19), but further to the left there are nothing but surface markings or lines in some of which there are the mouths of mucus pit organs. However, on the



"neck" of the right head there is a distinct groove (Figs. 7 and 8) connecting the hinder top edges of each gill-cover. On the extreme left, this groove is fully 3 mm. deep, but it grows progressively shallower toward the right, and, after crossing the mid-dorsal region, it becomes shallower and shallower until it is hardly a millimeter deep. Set in this, especially on the left are the openings of mucus pit organs. This ring-like constriction in the neck region of the right head is comparable to what is often seen on the back of the neck of a fat man where folds of flesh are separated by a constriction. The same constriction may be noted in the "ring" around the wrist of an over-fat baby. Possibly this "ring" in this fish may be due to the same cause, for the fish is plainly over-fat.

Here again it must be noted that the corselet-like covering of skin on the heads of this monster is entirely unlike that covering the body (Figs. 7 and 8, pls. 18 and 19), and is sharply delimited from it. This we found in Fish No. III, but the condition here is more accentuated than in the smaller fish. Both the cause and the meaning of this curious head covering are mysteries to me.

Midway between the declivity of the fork and the anterior base of the dorsal is a concavity. This is seen in Figs. 7 and 8, pls. 18 and 19. Behind this our fish seems normal above. Where the paired anterior vertebral columns unite cannot be said here, but one must think this point in the region of the dorsal fin. The lateral lines of each outer side seem entirely normal.

In ventral view (Fig. 9, pl. 19), it is apparent that the isthmus connecting the two heads is much further forward than is the junction of the two heads on the dorsal surface. Also emphasized in this view is the fact that the left head is the main head and the right one the subordinate. The deep groove in front of the isthmus has at its inner surface the plane of origin of the two inner pectorals—the left below the other. The groove becomes a deep cleft behind each inner opercular region—this to permit exit of respiratory water. On the inner side of the left head, the cleft becomes a chasm at the bottom of which (in shadow in Fig. 9, pl. 19), the inner edges of the left head gills are found. Note also that the outer gills of both heads are visible.

Seen in ventral view, this monster seems fairly normal from the pectoral fins backward. The right pectoral fin is so large and so forwardly placed that it has slightly outpushed the outer hinder edge of the gill-cover of the right head. The left outer pectoral arises a bit forward of the outer right fin, but if dividers are used it will be found

that on comparing distances from the anterior base of each fin to tip of the lower jaw of its head, the left head distance is about 4 mm. greater. The lower jaw of each head abounds in mucus pits. Those of the right head are especially prominent, those of the inner half-jaw of the left head are less so and those of the outer left jaw are comparatively small and inconspicuous.

The pelvic fins also present some slight anomalies which are not visible unless the fins are pulled away. The right pelvic is the larger and longer, and has at the outer edge of its base a large thick crumpled fold of flesh in the very spot where some fishes have an accessory scale. The left pelvic is smaller than the other by about one-third and has a smaller and straight fleshy mass on the outer edge of its base. The left fin is not only smaller but its base is narrower and is placed somewhat forward of that of the right pelvic. The unpaired anal and caudal fins present no abnormalities.

The X-ray picture (Fig. 10, pl. 19) confirms the earlier conclusion that the fork is placed far forward—just back of the depression seen in Fig. 7, pl. 18. Entirely lacking in external indication is the queer kink in the vertebral column about under the forward base of the dorsal fin. No cause for this is apparent. The left head plainly continues the axis of the body.

In this specimen as in the preceding ones, counts of vertebrae are difficult. On the left side there are 12, on the right *c.* 10. Next comes a region where the vertebrae, 6 or 7 in number, seem to be doubled and possibly partially fused. In the region of the bend are 6 or 7 seemingly crumpled and possibly enlarged vertebrae. Behind this section, there seem to be 6 fused vertebrae as indicated by the crowded 6 ribs on the right side. Behind this region, in the tail proper I find 25 vertebrae visible, with possibly 3 or 4 at the base of the tail invisible.

#### THE CAUSES OF DOUBLE-HEADEDNESS IN FISHES

The cause of this teratological condition in fishes is still a mystery. Various theories have been proposed but none offers an explanation satisfactory to me. No attempt will be made herein to review all these theories and only brief mention of the chief ones will be made. At the close of this section reference will be made to a book in which most of them are extensively and ably discussed.

The earliest professional breeder of trout, and the first to note in any extensive way double-headed fish embryos, seems to have been Stephen Ludwig Jacobi in 1763. He wrote on fish culture and de-

scribed various kinds of fish monsters including double-headed and Siamese-twin forms. He noted that these all die at the end of four or five weeks when the yolk is absorbed, and gave it as his opinion that "double fish have been generated when two spermatric animalcules have slipped into the egg." Further on he averred that double fish and all like monsters result "when an egg is fructuated by more than one spermatric animalcule." This is today the opinion prevalent among our fish hatchery men. Jacobi's writings aroused much interest and have been translated and quoted down to comparatively recent times. He may well be called the founder of modern pisciculture.

Gemmill in his great work (1912) says: "There is strong reason for believing that the occurrence of double monstrosity is due in the main not to environmental factors but to conditions which are inherent in the fertilized germ cell." He recognizes that the production of twins has frequently been brought about experimentally in many cases in invertebrate ova and in some holoblastic vertebrate eggs by separation of individual cells or masses of cells in early stages of segmentation. He concludes, however, that such would be difficult to bring about in meroblastic fish ova where the early cells are cut out of a syncytium. Still he notes that such monsters have been produced in fish eggs by experimental methods. Later it will be shown that nature sometimes produces them.

Finally with regard to the matter of polyembryony, Gemmill says that: "The view has often been suggested that the blastoderm may be looked on as a stock, able to give rise vegetatively so to speak to more than one embryo." Then he concludes that: "More probably, however, in animals, twinning, double and multiple monstrosity, and polyembryony provide instances in which a common 'potentiality' has become realized, and beyond that are not necessarily connected by any nexus of direct or phylogenetic character."

Stockard (1921), in an extensive paper in which he sums up long years of experimental work, declares that double monsters may be produced by developmental arrests due to the lowering of the temperature or to the reducing of the oxygen supply. With regard to the blastoderm as a stock (suggested by Gemmill), he notes that the notches around the edges of the leaves of some plants have the power to give rise to buds and by analogy suggests that "At a certain place along the germ-ring in the fish's egg a peculiarly rapid cell multiplication begins and the embryonic shield with the axis of the embryo buds away from this place."

He thinks that probably there are numbers of such potential points, but that when one point has begun to proliferate cells the others are normally inhibited. "The origin of two embryonic axes or growing points on the germ-ring of the fish probably results from a rather mild or slight reduction in the normal developmental rate at the time of gastrulation or embryonic-shield formation." And this may be brought about by lowering the temperature or decreasing the supply of oxygen. Certain eggs after relief from low temperatures

resume their cleavage processes, form a typical blastoderm and begin the formation of a germ-ring, which indicates the commencement of gastrulation, but just here the degree of energy necessary for normal developmental processes is insufficient and a single embryonic bud is not formed with that normal rate of growth which suppresses the appearance of other embryonic buds. Therefore, instead of the one point proliferating at a disproportionate rate to form the embryonic shield, two such points are established with more or less equal rates of proliferation, both of which may be somewhat less active than the single one should be. The formation of two embryonic shields, or the initiation of two points of rapid gastrulation away from which will grow the axes of the embryos, is in fact the initial or primary step in double formations.

Stockard follows with a recital of his experiments and descriptions of the relatively few monsters produced while working with the eggs of *Fundulus heteroclitus*. Noting that cell proliferation, a process fundamental in the production of embryos, is a great oxygen-consuming process, Stockard carried on experiments in which the eggs were allowed to clump together with a reduction in the relative amount of oxygen available for each egg. Eggs were also placed in water from which the oxygen had been expelled by boiling. The results in the development of abnormal fish in both lots of eggs were directly comparable.

Stockard's experiments were with the very hardy eggs of *Fundulus*, and he recognizes that double-monster formation is more frequent in salmonid eggs. While this is probably due in part to crowding and deficient aeration, there does seem in these eggs to be some inherent tendency to form monsters. Here follows Stockard's own brief summary of his results.

By an interruption of development [by lowering the temperature or reducing the oxygen supply] during late cleavage stages, a considerable percentage of twins and double individuals may be produced. When the eggs of the sea-minnow, *Fundulus heteroclitus*, are subjected to temperatures of 5° or 6°C. during cleavage stages, development is al-

most stopped. On returning such eggs to a summer temperature, after several days' sojourn in the refrigerator, there will follow a high mortality, but many specimens will resume development producing a significant percentage of twins and a number of variously deformed conditions along with a good proportion of normally formed young fish.

Arresting or stopping development of the same eggs during the same developmental stages by diminishing the available supply of oxygen will be followed by closely similar results.

The eggs of the trout are naturally much more inclined to develop into double individuals than are those of *Fundulus*. When the oxygen supply during early development is not abundant, a great many twin and double trout specimens are frequently found to occur.

At this point I wish to set forth some personal embryological observations. In my study of the segmentation of the egg of the pipefish (1905), I found and figured in surface view and in sections, divided blastoderms. These would undoubtedly have given rise to Siamese-twin embryos. Furthermore I have seen drawings of a two-headed very young pipefish. These eggs are carried, it will be recalled, in a marsupium under the caudal region of the male pipefish, and it may be thought this unusual situation had something to do with the production of divided blastoderms, since the eggs are crowded and since their oxygen supply must come by osmosis from the enclosing tissues. However, such abnormal eggs, so far as my three years' study went, were very few.

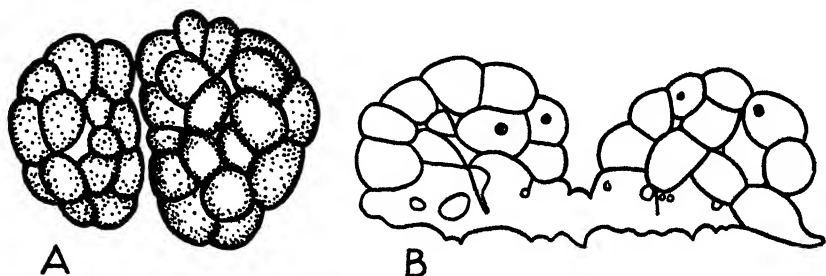
Furthermore, I found such divided blastoderms in the eggs of the toadfish attached to the inside of *Pinna* shells out in the harbor at Beaufort, N. C., in which the sea water circulated freely. These were referred to but not described in my article on the life history (1910, p. 1099) of this fish. I have also found Siamese-twin embryos in the orally-incubated eggs of the gaff-topsail catfish over which a constant current of water was moving (1918, Fig. 7, pl. III). Moreover I have in my possession a two-headed little fish of this form, and I have seen another. Furthermore a pair of Siamese twins of this form was once taken in the waters of eastern North Carolina, and figured and described by Churchill (1834).

These facts are all cited that the reader may know that two-headed forms and even Siamese twins among bony fishes are found in nature in both unusual conditions and in free water.

Let us now return to the divided blastoderms of the pipefish, portrayed in Text-fig. 4A and B. These separate half blastoderms are connected at their bases by the common syncytium out of which their

basal cells are being cut. If development had gone forward these half blastoderms would have produced Siamese-twin embryos like those of the gaff-topsail catfish referred to (1918, Fig. 7, pl. III). I have seen in fish hatcheries many such double monsters, and have now for description two sets of Siamese-twin dogfishes. These surely came from divided blastoderms such as are shown in Text-fig. 4A and B. It does not seem going too far to suggest that each half blastoderm may have arisen from each cell of the first segmentation stage, if only these cells by some agency were widely separated above but connected at the base by the syncytium.

In this same conjecture may be found the germ of an explanation of the formation of two-headed fishes. Let it be supposed that at the



TEXT FIG. 4. Divided blastoderm of the pipefish, *Siphostoma floridae*

A, surface view, syncytium not shown; B, sectional view, showing the two separated discs resting on the syncytium.

After Gudger, 1905.

first cleavage of the blastoderm, the two cells instead of being widely separated from front to back, were pulled apart on one edge only—the two being separated in front by a V-shaped cleft, but being in ordinary close juxtaposition at the end of the cleft. Then if segmentation went forward in reasonably ordinary fashion, there would result a sort of complex-compound blastoderm, the two parts joined at the hinder edge but having a cleft in front. Might not such an abnormal blastoderm develop into a two-headed fish? So far as I know this conjecture has never been put forward, but where so much is conjecture this has at least the interest of novelty.

Should the reader be interested enough to wish to go deeper into the subject of two-headed monsters, he will find that the whole subject of the nature, scope, and causation of twin formation has been admirably

treated by H. H. Newinan in his valuable book, "The Physiology of Twinning" (Chicago, 1923, 230 p., 70 text-figs., 12°). To this work, and especially to chapters IV and V, dealing with the various theories advanced to explain twin formation in fishes, the student is referred.

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NEW YORK CITY

Postscript.—Since this paper went to press, my attention has been called to an article, on double monstrosities in the embryos of the viviparous fish, *Gambusia*, by Thirumalachar of Mysore, India (Proc. Indian Acad. Sci., 1938, 7B, 317–322, 6 figs.). Among these anomalies were two sets of embryos united at the head region into monsters. One set was entirely symmetrical with a single compound head and two bodies and tails free and equal; the other had one head and one large and one small body. In explanation, the author says . . . "on account of the development in a confined space [in the maternal ovary], the two embryonic axes seem to have come together by their head ends and fused to some extent."

I cannot see this. The space was little more confined than that in the sub-caudal pouch of the pipefish. I cannot understand how the embryos of two eggs could have fused. These monsters must have each developed on one egg. Here we have one head and two bodies and tails—the reverse of the conditions in my two-headed, one-bodied and tailed trouts. To explain—reverse the separation in the two-celled stage, spread the cells apart behind and a one-headed, two-tailed monster will be formed.

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## PLATE 17

- Fig. 1. A 32-mm. two-headed Loch Leven Trout ( $\times 1\frac{1}{2}$ ) from Yosemite Hatchery,  
California. A, dorsal view; B, ventral view. Specimen by courtesy Mr.  
Archie Thompson.
- Fig. 2. A 45-mm. two-headed Eastern Brook Trout ( $\times 2$ ) from Yosemite Hatchery,  
California. A, seen from above; B, from below. Specimen by courtesy  
Mr. Archie Thompson.
- Fig. 3. A 53-mm. two-headed Eastern Brook Trout ( $\times 2$ ) from Yama Farms  
Hatchery, Napanoch, N. Y. A, dorsal aspect; B, ventral surface.  
Specimen by courtesy Mr. A. A. Townsend.
- Fig. 4. X-ray photograph ( $\times 2$ ) of the 53-mm. fish shown in Fig. 3. This was  
made (dorsal aspect) after the specimen had been twelve years in pre-  
servative. By courtesy Dr. H. A. Kelly.

## PLATE 18

- Fig. 5. The 90-mm. two-headed Loch Leven Trout ( $\times 1$ ) from Yosemite Hatchery,  
California. A, seen from above; B, from below. Specimen by courtesy  
Mr. Archie Thompson.
- Fig. 6. X-ray photograph ( $\times 1$ ) of the 90-mm. specimen shown in Fig. 5. By  
courtesy Dr. Howard A. Kelly.
- Fig. 7. Dorsal view of the 203-mm. two-headed Brown Trout ( $\times c. \frac{1}{2}$ ) from Mt.  
Shasta Hatchery, California. This is the largest two-headed teleostean  
fish ever figured and described. Reared by Mr. Elvin C. Anderson.

## PLATE 19

- Fig. 8. Head-on view of the 203-mm. monster ( $\times 1$ ) from Mt. Shasta Hatchery,  
California. Specimen by courtesy Mr. E. V. Cassell.
- Fig. 9. Ventral aspect of the 203-mm. two-headed monster ( $\times c. \frac{1}{2}$ ) from Mt. Shasta  
Hatchery, California. Specimen by courtesy Mr. E. V. Cassell.
- Fig. 10. X-ray photograph ( $\times c. \frac{1}{2}$ ) of the 203-mm. fish from the Mount Shasta  
Hatchery, California. By courtesy Dr. H. A. Kelly.









PLATE 18





PLATE 19





## POLYCLADS OF BEAUFORT, N. C.

By A. S. PEARSE and J. W. LITTLE

### PLATES 20-23

During the summer of 1937 and 1938 collections were made in the waters near Beaufort, N. C. Work was carried on in the Biological Laboratory of the United States Bureau of Fisheries. We give hearty thanks to the director, Dr. H. F. Prytherch, and other members of the staff for assistance. Ten species of polyclads have been found. As all but one of these have been previously described we give only a brief diagnosis of each, with a figure showing its appearance while alive, and notes on distribution and habits in the Beaufort Region. *Hymania prytherchi* is described as a new species. A key for the identification of the species found is included in this paper. All our specimens have been deposited in the United States National Museum.

#### Order POLYCLADIDA

##### Suborder ACOTYLINA

##### Section Craspedommata

##### Family Discocelidae

##### *Discocelis grisea* Pearse

#### Fig. 1

This polyclad was originally described from Florida. When alive its movements are quick and the anterior end is somewhat wider than the remainder of the body. The largest individual measured was 18 mm. long and 5 mm. wide when extended. The narrow pharynx is folded into about 10 pairs of lobes; 10 pairs of branched, lobate caeca arise from the median stem of the enteron and extend to the margins of the body; mouth is ventral, just anterior to the posterior border of the pharynx. Close behind the mouth the prostate gland and penis are enclosed in a pyriform sheath, with 2 to 4 lateral appendages; 2 coiled vasa deferentia from the prostate lie close beside the pharynx; at about the posterior third of the pharynx each gives off a lateral branch which coils posteriorly and fuses with the one from the opposite side behind the accessory uterine organs. The vagina



behind the single genital pore is surrounded by shell gland follicles; two lateral, longitudinal uteri extend forward from the shell gland close beside the pharynx; behind the shell gland a slightly sinuous median duct connects with a pair of transverse accessory uterine organs. Numerous ovaries and testes are distributed in a ring around the pharynx and genital ducts. Marginal eyes are most abundant toward the anterior end, and in young specimens may be absent altogether at the posterior end. Two groups of eyes, cerebral (about 12) and lateral (about 20), are present. The color is gray, with a light median streak and radiating bands; or gray around the margin and somewhat speckled tan in the middle.

Five representatives of this species were collected at Beaufort; 2 September 9, 1937, from shells dredged in Bogue Sound; 1 June 7, 1938, from shells dredged inside Shackleford Bank; 1 July 1, 1938, from algae on mud flats; 1 July 11, 1938, from algae collected off Cape Lookout.

Family Stylochidae  
*Eustylochus meridianalis* Pearse

Fig. 2

Body elongate-elliptical; 24 by 11 mm. when extended. Tentacles slender, conical, 0.6 mm. long, with eyes extending to distal sixth, about a seventh of length of body from anterior end. Mouth ventral, about in middle of median line; pharynx a little less than half as long as body; with anterior, posterior, and about 6 paired lobes; enteron with median stem and 8 or more pairs of lateral branches. Brain largely or wholly posterior to the bases of the tentacles, so that the cerebral eyes lie between or posterior to the tentacles; marginal eyes extending through anterior fifth or to posterior end, decreasing in size and number posteriorly; eyes vary in number: cerebral 6-54, frontal 4-44, tentacular 22-150, marginal 290-860. Genital pores very close together and less than a thirtieth of body length from posterior end; a large, clear, pyriform seminal vesicle lies just in front of them and is quite apparent even in living specimens. Color reddish brown, or sometimes gray; the dorsum is finely maculate.

This species ranges from Texas to Maryland. It is commonly associated with barnacles and oysters, and feeds on both. At Beaufort it was found throughout the summer associated with barnacles on bridge piles. On June 29, 1938, seven specimens were taken from old shells dredged off Cape Lookout.

*Stylochus zebra* Verrill

Fig. 3

This large (40 by 12 mm.) and striking species is readily recognized by its prominent cross bands. Nuchal tentacles are situated at the end of the anterior ninth of the body; they are short and filled with numerous black eyespots; there are also a pair of cerebral eye-clusters and numerous marginal eyes which gradually decrease toward the posterior end. Pharynx, elongated; with eight or ten pairs of lateral lobes; mouth opposite third pair of lobes. Two genital pores lie about a seventh of body length from posterior end. Color above yellowish-brown to chocolate-brown crossed by numerous light stripes.

Two specimens were collected during the summer of 1938; one June 17 from algae collected by Dr. W. C. George on the east shore of Shackleford Bank and another June 23 from a hermit crab taken from Bogue sound.

## Section Schematommata

## Family Leptoplanidae

*Leptoplana augusta* Verrill

Fig. 4

Body when extended long and narrow (16 by 6 mm.), flexible; front usually rounded and posterior end often notched; margins flexible, often undulated or curled. Cerebral and dorsal eyes often blend so as to make two fusiform, lateral groups. Pharynx long, with about 12 pairs of lateral lobes; mouth somewhat posterior to its center. The reproductive organs surround the pharynx, forming an opaque elliptical zone; the genital apertures are about a fifteenth of body length from posterior end. Color light brown, often darker in middle and at margins.

In the collections of the United States National Museum are specimens from the Baffin Bay and Florida. We have added one found among shells and ascidians in Bogue Sound, September 9, 1937.

*Stylochoplana floridana* Pearse

Fig. 5

When alive this species is quite active. It moves about jerking the margins of its body and when disturbed often darts about like a wriggling fish. Body widest across anterior and tapering to the bluntly pointed posterior end. Pharynx narrow, with about ten pairs of

lateral folds. Tentacles about 0.1 mm. long, each bearing 5 or 6 eyes; 6 eyes lie on each side lateral to the brain, and 5 on each side between and posterior to the bases of the tentacles. A globular seminal vesicle lies close to the posterior border of the pharynx and the genital opening is 0.4 mm. behind it. Color delicate, pale green. Many of the specimens collected at Beaufort were larger (12 by 4 mm.) than any that had been found in Florida (8 by 3 mm.).

This delicate little polyclad is common about Beaufort. It is usually associated with algae and has been obtained from mud flats and deeper waters near the United States Bureau of Fisheries Laboratory, and from dredged old shells along Shackleford Bank and in Bogue Sound.

Family Stylochocestidae

*Euplana gracilis* (Girard)

Fig. 6

Body when extended about 6 times as long as wide (10.3 by 1.9 mm.). The eyes are very few and arranged in 4 pairs lateral to the brain. Mouth about a third of body length from anterior end, in center of pharynx. There are about 12 pairs of bifid enteric caeca lateral to the pharynx and uteri, 12 more behind the transverse connecting loop of the uterus, and 5 extend forward ventral to the eyes and brain. Behind the uterus the enteron consists, besides marginal caeca, of a median and 2 lateral trunks which are connected by about 6 transverse canals. The uteri are distinctive: they are swollen and somewhat twisted in gravid individuals; a transverse loop connects them posterior to the vagina, just behind the pharynx; they taper anteriorly and may be traced forward to the middle of the pharynx. Body is unpigmented ventrally but the dorsum is flecked with gray-brown, with the enteron and other organs visible; general appearance, delicate light brown.

One specimen was collected from among ascidians scraped off the railway bridge near Piver's Island, June 2, 1938.

Section Emprosthommata

Family Cestoplanidae

*Oculoplana whartoni* Pearse

Fig. 7

Body flat, long and slender, in living specimens at least eight times as long as wide (largest, 36 by 3 mm.), blunt and rounded at both ends; at the posterior end is a weak, poorly defined adhesive organ. Enteron

extends throughout body, nearly 100 pairs of lateral twigs leave it; median stem extends forward and branches along the anterior margin; mouth at anterior end of posterior fifth of body; pharynx frilled, slender, two-thirds of it behind the mouth. Genital apertures about a ninth of body length from posterior end, just behind the pharynx. Color pale yellowish-white, without pigment; the yellowish enteron shows through the integument; some individuals have a delicate pinkish tint.

Throughout June 1938 this polyclad was not uncommon on old shells dredged along the edge of Shackleford Bank and in Bogue Sound at depths of 1 to 2 fathoms. A very large specimen was taken from shells off the Cape Lookout jetty July 8, 1938.

Suborder COTYLINA

Family Euryleptidae

*Hymania* n. gen.

With the characteristics of the Family Euryleptidae as defined by Lang (1884) and Bresslau (1928-1930). It resembles the genera *Eurylepta* and *Cycloporus* somewhat; but differs from the former in the anastomosis of the enteric twigs. It has unique features in the anterior bifurcation of the uteri, the formation of two uterine canals which fuse posterior to the median enteric stem and open ventrally through a pore, and in the posterior fusion of the vasa deferentia posteriorly and their prolongation as a median caecum. The genus is named for Dr. Libbie H. Hyman, who has made notable contributions to knowledge of turbellarians in America.

Type *Hymania prytherchi*.

*Hymania prytherchi* n. sp.

Figs. 10-13

Though this species differs in some respects from Lang's (1884) figures of other species in the genus *Eurylepta*, it agrees with his characterization of that genus. Its noteworthy points of disagreement are as follows: (1) uteri do not fuse but end blindly at posterior end and are bifid anteriorly and (2) the vasa deferentia fuse posterior to the median stem of the gut and are then prolonged into a short caecum. The present species is quite different from *Eurylepta maculosa*, described by Verrill (1893) from Massachusetts, in size, color, and number and arrangement of the eye spots.

The largest specimen examined measured 29 mm. long and 12 mm. wide when crawling and extended; the type measures 15 by 11.2 mm.

and the cotype 15.6 by 10.4 mm. after being stained and mounted. The body is flat, ellipsoidal in outline with the anterior end somewhat truncate, and notched where the tentacles arise. The margins are always more or less crinkled (Fig. 10) and undulatory movements of the margins apparently help in locomotion. The marginal tentacles are rather close together (1.4 mm.), conical, flattened somewhat and slightly grooved at their bases on their antero-ventral surfaces, and about 3.0 mm. long. On the dorsal surface low protuberances indicate the position of the pharynx, just posterior to the brain, and behind this on either side of the median line those caused by the swollen uteri.

Structures along the median line (Fig. 11) are at the following distances from the anterior end in millimeters: brain 1.7—1.8; mouth 4.0; pharynx 3.7—6.9; male genital pore 9.4; female genital pore 10.7; ventral sucker 15.5—16.5; median enteric stem 6.8—21.7; vasa deferentia 5.3—23.7; caecum at posterior end of fused vasa deferentia 23.7—25.2; uterine glands 12.2—14.3; posterior end 29.

Eyes (Figs. 10, 11, 12) on the two sides of the body of the type specimen number as follows: tentacular 79 : 74, intertentacular 17 : 16, cerebral 39 : 36. Those on the tentacles are confined to the proximal half. The number of eyes varies with age and the three groups of cerebral eyes figured number 54, 67, and 116.

The enteron consists of a tubular pharynx enclosed in a sheath, a median enteric stem about 1.5 mm. wide, and about seven pairs of branched lateral extensions which reach close to the margins of the body. The pharynx when at rest is much wider at the anterior than at the posterior end. The lateral enteric twigs anastomose, especially toward the posterior end.

The male genital system (Fig. 11) begins at the genital pore 2.3 mm. behind the pharynx, though the position may vary somewhat with the degree of contraction of the body. The ejaculatory duct makes a loop backward (0.6 mm.) and then forward (2.2 mm.) to the junction of the two vasa deferentia which enter from each side; into it open a plump, ovate seminal vesicle and a slender, pyriform prostate gland. The vasa deferentia coil along either side of the body lateral to the oviducts, fuse behind the enteric stem, and are prolonged into a caecum. Numerous small testes (*te*) are distributed among the lateral enteric twigs in two crescentic lateral areas. From the female genital pore a short sinuous vagina leads posteriorly (1 mm.) to two transverse uterine ducts (*ud*); about it are the slender radiating follicles of the shell gland. The transverse uterine ducts extend laterally 2.6 mm. to the plump

spindle-shaped uterine glands (*ug*); three ducts enter each on the posterior side (Fig. 13), the inner two connect with a uterus which ends blindly near the posterior end of the enteric stem, the outer one extends back behind the enteric stem and fuses with the one from the opposite side. Ovarian follicles (*o*) are about twice the size of testes and have about the same distribution.

The color of this polyclad is orange and appears to come largely from the digestive system. It is much like the color of the interior of ascidians among which the worm usually lives. The dorsum is much darker than the venter, which is cream-colored. The color of the dorsum grows gradually lighter toward the margins of the body. It tends to be pink over the pharynx and in gravid individuals the paler uteri show through the integument. There is no pigment over the brain, except that in the eye spots.

This species is quite common during the summer on piles among ascidians (*Styela plicata* Lesueur), where it is often associated with *Oligoclado floridanus* Pearse. It laid eggs in the laboratory during July and August. The species is named for Dr. H. F. Prytherch.

Type: U. S. Nat. Mus.; Beaufort, N. C.; July 7, 1938; A. S. Pearse, collector.

*Oligoclado floridanus* Pearse

Fig. 8

This cotylean may measure 18 mm. long and 8 mm. wide when crawling and extended. Tentacles at anterior end slender, acute, with eyes in proximal half, 1.3 mm. long. Color of dorsum brown, with a purplish median band and a cream-colored margin; brown apparently largely due to enteron; venter light brown with a light band due to genitalia through median region. About 80 eyes lie between the bases of the tentacles, about 50 occupy the proximal half of each tentacle, and about 70 eyes are arranged in the form of a horseshoe with the opening posterior or when contracted are close together in an elongate mass. Pharynx tubular, immediately posterior to brain; from it a median enteric stem extends to anus; 3 pairs of lateral, branched caeca leave the stem in its anterior half and extend to all margins of body; on either side of the anus two tubes extend forward to the anterior ends of 2 lateral glandular organs. Male genital pore is median, at posterior ninth of pharynx; the female pore is about 1 mm. posterior to that, and the ventral sucker 1.5 mm. posterior to the female pore.

At Beaufort this species was often associated with ascidians (*Styela*

*plicata* Lesueur) on wharf piles, but was at times found on shells at a depth of a fathom or two. During June specimens kept in the laboratory often laid eggs on the sides of dishes.

### Family Prosthiostomidae

#### Fig. 9

#### *Prosthiostomum lobatum* Pearse

Body of living specimens slender, ribbon-like, 17 by 2.7 mm.; wider in front, tapering toward the pointed posterior end. There are about 106 eyes in adult individuals—about 70 marginal, 2 intermediate, and 35 cerebral; at the anterior end there is usually a space about 0.15 mm. wide without eyes and on either side of this eyes extend, about two-thirds of them anterior to the brain; cerebral eyes are usually arranged as a horseshoe or a V with the opening directed posteriorly. The enteron consists of a median stem and about 22 pairs of lateral branches, the twigs of which extend to near the margin throughout the body; pharynx often coiled within its sheath, and often thrown out of body when worms are placed in fixatives, but in living worms rests longitudinally and is indicated by a median ridge. Male genital pore immediately posterior to pharynx; female pore 0.2 to 0.3 mm. behind it, and the sucker about the same distance behind that. Color: unpigmented except for the eyes; living specimens appear cream-color or gray-white, and darker yellow toward the median line where internal organs show through the integument.

This slender worm at Beaufort was often associated with sponges, but also occurred at times on old shells and oysters, and with pile animals.

#### KEY TO TEN SPECIES OF POLYCLADS WHICH OCCUR AT BEAUFORT, N. C.

- 1 (14) Without sucker behind female genital aperture; pharynx usually lobate, sometimes cylindrical; without marginal tentacles; no groups of eyes on anterior margin..... Suborder Acotylinea
- 2 (7) With marginal eyes; uteri never fused anterior to pharynx; body not ribbon-like..... Section Craspedommata, 3
- 3 (4) Nuchal tentacles absent; pharynx long, central, frilled; genital openings near pharynx; color gray with radiating light streaks and lighter median band..... *Discocelis grisea* Pearse
- 4 (3) Nuchal tentacles present..... 5
- 5 (6) With 2 clearly separate genital openings at least a seventh of body length from posterior end; body 30 to 40 mm. long and 10 to 12 mm. wide; yellowish brown with numerous transverse light stripes

*Stylochus zebra* Verrill

- 6 (5) With genital openings close together and less than a twentieth of body length from posterior end; size 24 by 11 mm., color reddish or gray  
*Eustylochus meridianalis* Pearse
- 7 (2) Without marginal eyes or body ribbon-like with eyes around whole margin..... 8
- 8 (13) Without marginal eyes and eyes that are present far from frontal margin; Section Schematommata..... 9
- 9 (12) Uteri fused anterior to pharynx..... 10
- 10 (11) No tentacles, body elongated; with about 12 pairs of lateral pharyngeal lobes; color light brown, with darker median streak; length 12 to 16 mm. by 4 to 6 mm..... *Leptoplana angusta* Verrill
- 11 (10) With nuchal tentacles; anterior end of body wide, rounded and posterior end pointed; very active, often swim; delicate green in color  
*Stylochoplana floridana* Pearse
- 12 (9) Uteri not fused anteriorly, but fused posterior to pharynx; body when extended 6 times as long as wide; mouth and pharynx in anterior half of body..... *Euplana gracilis* (Girard)
- 13 (8) With marginal eyes (none in European species of this section); pharynx and male genitalia near posterior end and latter directed forward; Section Emprostommata... .. *Oculoplana whartoni* Pearse
- 14 (1) With a sucker behind genital pores; often with marginal tentacles; pharynx folded, frilled, or tubular, Suborder Cotylina, 15.
- 15 (18) With a pair of slender, conical tentacles on anterior margin; pharynx short and tubular... .. 16
- 16 (17) Enteron with an anus at posterior end of its median stem; body 18 by 8 mm.; brown with median purplish band ... *Oligoclado floridanus* Pearse
- 17 (16) Without anus; body 29 by 12 mm.: color orange  
*Hymania prytherchi* n. sp.
- 18 (15) Without tentacles; pharynx long and tubular; body 17 by 2.7 mm., ribbon-like.... .. *Prosthiostomum lobatum* Pearse

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## EXPLANATION OF PLATES

## PLATE 20

Figs. 1-9. Nine species of polyclads to show appearance when alive.

## PLATE 21

*Hymania prytherchi* n. sp.

Fig. 10. Dorsal view of living specimen.

Fig. 11. General anatomy.—*c*, caecum at posterior end of fused uterine ducts; *e*, branch of enteron; *m*, mouth; *me*, median stem of enteron; *o*, ovarian follicles; *t*, tentacle; *te*, testes; *u*, uterus; *ud*, uterine duct; *ug*, uterine gland; *up*, pore at fusion of uterine ducts; *vd*, vas deferens; ♂, male genital pore; ♀, female genital pore.

Fig. 12. Three groups of cerebral eyes and a portion of a brain.

Fig. 13. Left uterine gland (*ug*) and connections of uterine ducts.

## PLATE 22

Figs. 14-19. Reproductive systems of polyclads: *es*, eyes; *o*, ovaries; *p*, pharynx; *pe*, penis; *pg*, prostate gland; *ps*, penis sheath; *s*, sucker; *sg*, shell gland; *sr*, seminal receptacle; *sv*, seminal vesicle; *t*, testes; *u*, uterus; *v*, vagina; ♂, male genital pore; ♀, female genital pore; *vd*, vas deferens; *ed*, efferent duct.

Fig. 14. *Stylochoplana floridana*.

Fig. 15. *Stylochoplana floridana*, penis.

Fig. 16. *Prosthlostomum lobatum*.

Fig. 17. *Stylochoplana floridana*.

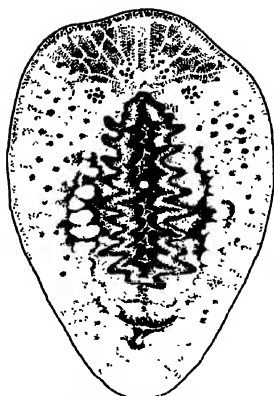
Fig. 18. *Eustylochus meridianalis*.

Fig. 19. *Oculoplana whartoni*.

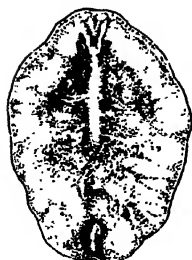
## PLATE 23

Figs. 20-22. Sagittal sections of three polyclads: *b*, brain; *c*, caecum at end of fused uterine ducts; *e*, enteron; *m*, mouth; *p*, pharynx; *pg*., prostate gland; *ps*, penis sheath; *s*, sucker; *sr*, seminal receptacle; *sv*, seminal vesicle; *up*, uterine pore; *v*, vagina; *vd*, vas deferens; ♂, male genital pore; ♀, female genital pore.

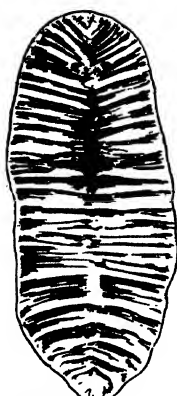
# PLATE 20



1. *Discocelis grisea*



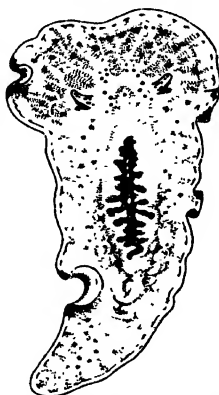
2. *Eustylochus meridionalis*



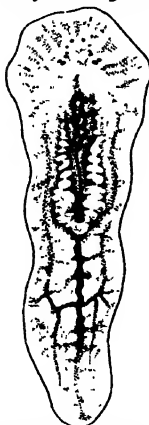
3. *Stylocheus zebra*



4. *Leptoplana angusta*



5. *Stylochoplana floridana*



6. *Euplana gracilis*



7. *Oculoplana whartoni*



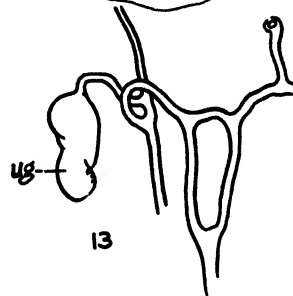
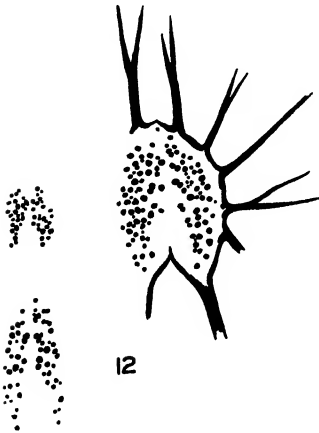
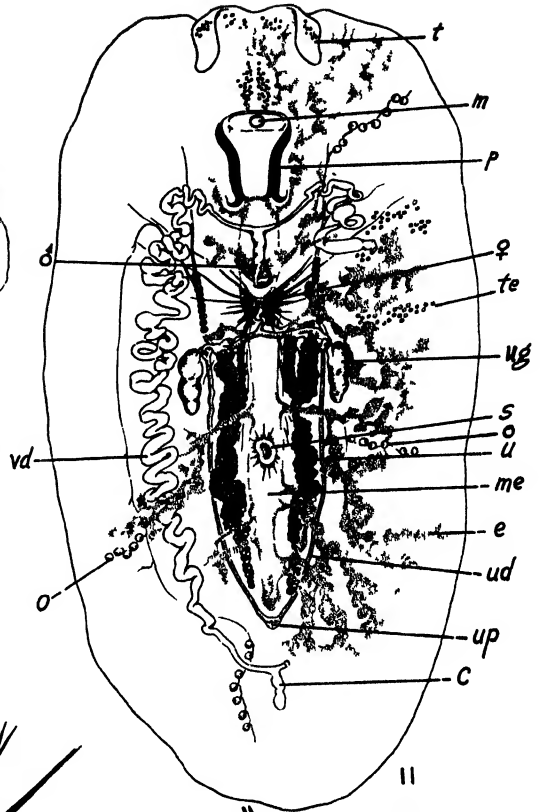
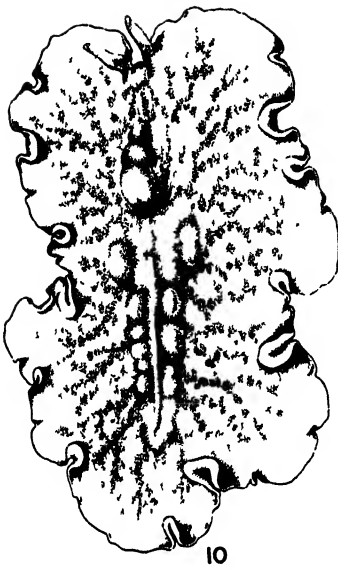
8. *Oligoclado floridanus*



9. *Prosthiostomum lobatum*



# PLATE 21





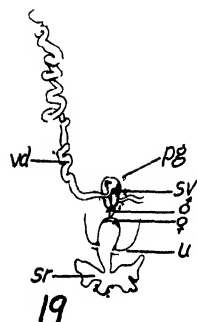
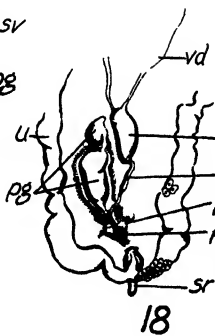
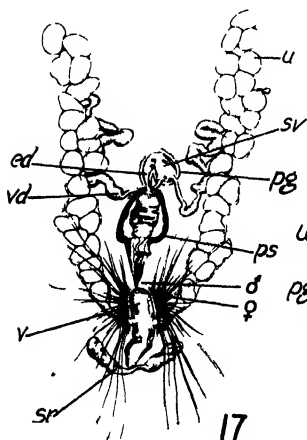
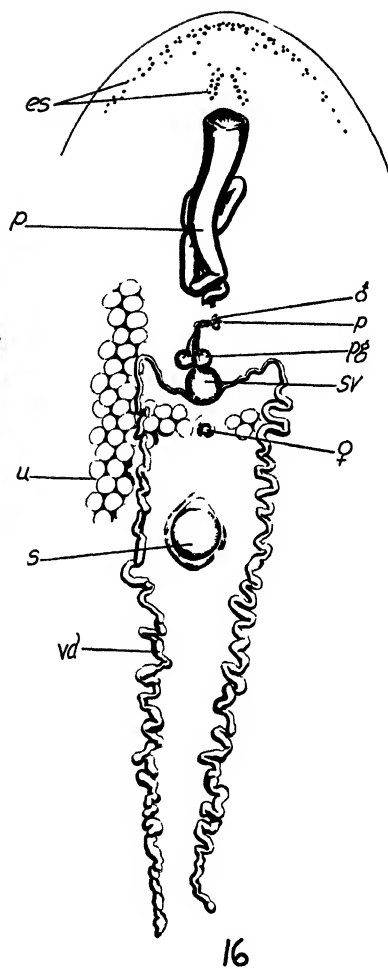
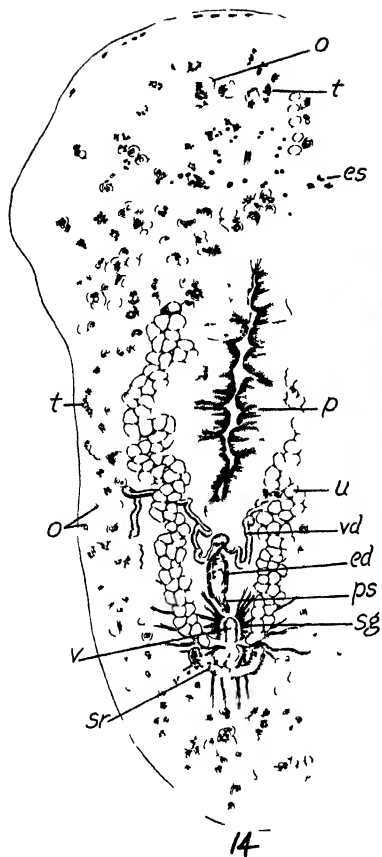




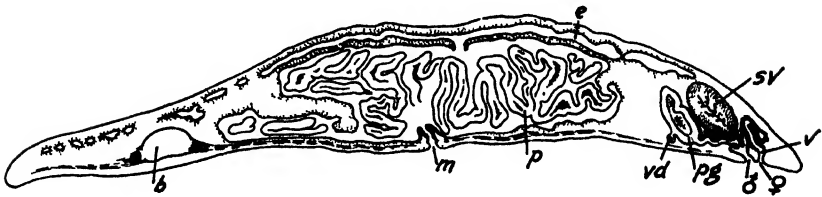
PLATE 23



20. *Hymania prytherchi*



21. *Stylochoplana floridana*



22. *Eustylochus meridionalis*





# THE LANCET FISH, ALEPISAURUS FEROX, ON THE NORTH CAROLINA COAST

By H. H. BRIMLEY

## WITH ONE TEXT FIGURE

On April 7, 1938, a specimen of this species was captured alive in the surf near Oregon Inlet, Dare County, N. C., by Mr. S. A. Walker, Superintendent of the Pea Island Game Refuge. The capture was written up in the Raleigh News and Observer of April 8, the article being illustrated by two photographs, neither of which showed the creature's tail. This omission was unfortunate, as it made the identification of the specimen by those who had not seen the fish practically impossible. It was only after a photograph showing the tail, together with the dried head of the fish, had been submitted to Dr. E. W. Gudger, of the American Museum of Natural History, New York, that a definite identification was made.



This specimen measured 57 inches in length. The species is slender-bodied with a long and high dorsal fin and a deeply-forked tail. The width of the tail of this specimen was given as 8 inches. The dried head—as illustrated—is  $8\frac{1}{4}$  inches in length. When secured the stomach of the fish was noticeably distended but, when lifted by the tail, most of the stomach contents slid out of its mouth. None of the

food so disgorged was saved but Mr. Walker stated that all of it seemed to consist of fish common to our waters.

The dried head and the fragmentary tail are now in the State Museum, together with several photographs of the specimen in the flesh.

The tooth formula is remarkable. In the illustration of the dried head one of the long, dagger-like teeth of the upper jaw is missing but the longest one shown in the photograph measures  $1\frac{1}{2}$  inches in height above the gum. It is keen-edged as well as sharp-pointed and dagger-shaped, the other similar teeth in both jaws having the same characteristics. The saw-like teeth situated in the hinder part of the jaws project about a quarter of an inch above the gum, also sharp-pointed and keen-edged. The whole layout constitutes a terribly efficient instrument for seizing and cutting the living forms on which the species feeds.

It is interesting to note that Mr. Walker, who captured this specimen, had previously picked up a fish of this species not far from the same place, on May 11, 1937, the two specimens being of approximately the same size. Not realizing its rarity, the first one was left on the beach.

*Alepisaurus ferox* is regarded as a deep-sea species, most frequently recorded from depths of 100 to 200 fathoms with at least one specimen from 275 fathoms. As a possible point of interest it may be noted that the pressure at the respective depths indicated amounts to 260, 520 and 715 pounds per square inch. However, there are records of its occurrence in comparatively shallow water along the Aleutian Islands.

Dr. E. W. Gudger, of the American Museum of Natural History, informs me that not more than a dozen specimens of this species have been recorded from both coasts of the United States. The two noted above give *Alepisaurus ferox* a place in the list of North Carolina fishes.

N. C. STATE MUSEUM,  
RALEIGH, N. C.,  
SEPTEMBER 19, 1938.

# THE OVERWINTERING OF UREDINIOSPORES OF PUCCINIA GRAMINIS TRITICI IN NORTH CAROLINA

By ALBERT F. THIEL

WITH 5 TEXT FIGURES

## INTRODUCTION

There are two possible primary sources of stem rust (*Puccinia graminis* Pers.) in the United States: aeciospores from susceptible barberries, and overwintering urediniospores. That susceptible barberries become infected with the aecial stage of stem rust, in the central and northern states, and serve as centers for the spread of rust has been demonstrated by Bulger (2), Thiel (12), Melhus and Smith (6), Leer (5), Stakman (9), and others. The writer knows of no record of the spread of rust from barberries in the states south of Virginia, Ohio, Indiana, Illinois, Missouri, and Kansas.

From 1918 to the present time the United States Department of Agriculture, cooperating with several north-central and eastern states, has conducted a vigorous barberry eradication campaign. During the period of 1918-1936, slightly over one hundred million bushes and seedlings were destroyed from 109,476 properties (Fig. 1).<sup>\*</sup> Of this total number, 59,214,869 bushes, or over half of the bushes destroyed in the United States, were found in Virginia. The destruction of so large a number of barberry bushes from the wheat belt and adjoining states has reduced materially the possibility of infected barberries initiating stem rust epiphytotics.

The overwintering of urediniospores of stem rust has been studied rather extensively in the Mississippi Valley and in the north-central states. Baringer (1), in Ohio, was unable to find any evidence of urediniospore overwintering; while Walker and Thompson (13), in Wisconsin, conclude that "Practically all red spores perish early in the winter." Durrell and Lungren (3), working in Colorado, and Peltier and Thiel (8), in Nebraska, all obtained similar results. Stak-

<sup>\*</sup> Data obtained from a report on the progress made in Barberry Eradication during the years 1918-36. U. S. Dept. of Agr. Bureau of Entomology and Plant Quarantine.

man (10), on the other hand, has reported their overwintering in southern Texas, and Peltier and Thiel (8) and Wallace (14) have presented evidence which suggests a rather general northward migration of stem rust from such overwintering urediniospores.

The results of the investigations made by these workers and others demonstrate convincingly that the early spring source of stem rust inoculum in the northern and north-central states comes from aeciospores of infected barberries, and from the northward migration of rust initiated from overwintered urediniospores.

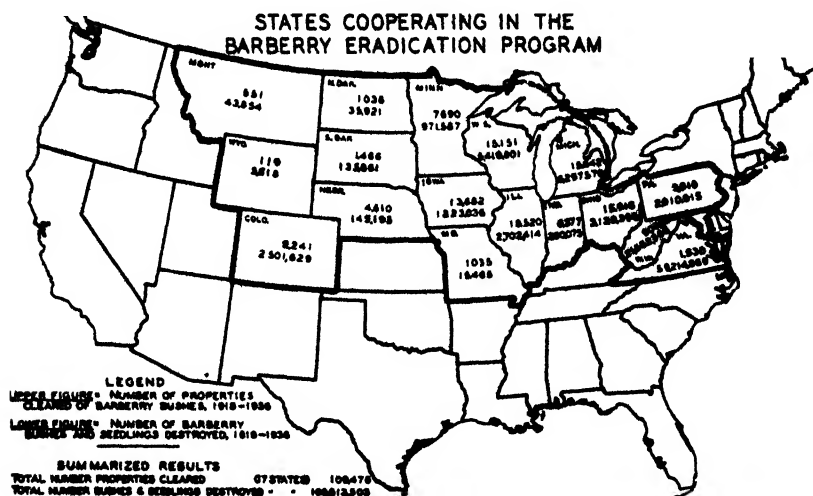


FIG. 1. Map showing the states in the Barberry Eradication area, the total number of properties cleared of barberry bushes, and the number of barberry bushes and seedlings destroyed. 1918-1936

The spring source of inoculum of stem rust in North Carolina has not been definitely determined. Does the native barberry, *Berberis canadensis*, become naturally infected in this state and initiate a primary source of rust? Should the barberry become infected with stem rust it would not only be responsible for a spring source of rust but it would also be the breeding ground for new forms of stem rust. Stakman (11) and Newton (7) have reported the hybridization of such new forms of rust on the barberry. Does the primary inoculum come from overwintering urediniospores in this state or from a northward migration of urediniospores from the states to the southwest of North Carolina?

This paper attempts to answer the latter question and reports the results of experiments and field observations on the overwintering of urediniospores of stem rust of wheat. An answer to the first question will be attempted in a later paper. This study is based on germination tests during the winters of 1935 to 1938, and on field observations during the years 1934 to 1938.

#### THE DISTRIBUTION AND IMPORTANCE OF WHEAT AND OTHER SUSCEPTIBLE STEM RUST HOSTS IN NORTH CAROLINA

Wheat is cultivated in nearly every county of the state. The largest acreages are confined to the piedmont counties of Davidson, Rowan, Iredell, Randolph, Stanly and Union (Fig. 2). The total wheat acreage

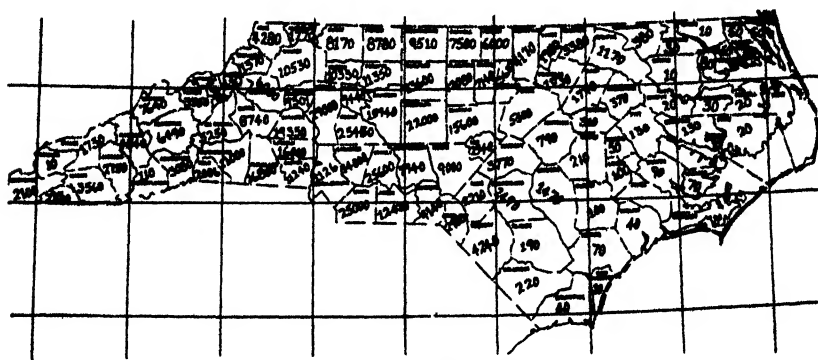


FIG. 2. Map of the state of North Carolina showing the wheat acreages in each county. 1936

in 1936 was 520,000.<sup>1</sup> In 1866 North Carolina's wheat production was less than two million bushels, while in 1936 it was slightly above five million bushels. The wheat plant is the most important host for the overwintering of the urediniospores.

Barley, which is also susceptible to stem rust of wheat, is not a very important crop in North Carolina. The land planted to barley in 1937 totalled about 9000 acres.

There are several native grasses in North Carolina that are susceptible to the rust form which attacks wheat. Those which were observed to be infected with stem rust are: *Hordeum pusillum*, *H. vulgare*, *Hystrix patula*, and *Elymus virginicus*. These grasses can usually be

<sup>1</sup> Data obtained from the Farm Forecaster for November, 1937. North Carolina Department of Agriculture, Raleigh.

found infected with rust during the early summer. They serve particularly as hosts during the summer when the wheat crop has matured. They are, therefore, important in the overwintering of the rust fungus.

#### OVERWINTERING OF UREDINIOSPORES

During the months of October and November, extensive observations were made for uredinial material on the fall-sown wheat and on volunteer wheat in Randolph, Chatham, Alamance, and Guilford counties. Infected wheat plants were extremely rare and it was never possible to find more than a few uredinia on the leaves. These infected plants were marked by a stake and their location recorded in order to facilitate finding them on succeeding visitations. A few infected leaves were collected twice a month from October to March and were taken to the laboratory where the spores were tested for their viability. The hanging-drop method and van Tieghem cells were used in making the germination tests. Triplicate sets of experiments were made, and after a period of twenty-four hours, the number of germinating spores and non-germinating spores were counted and the average percentage of viability determined for a given period.

The results of the germination tests during the fall and winter months are shown in figure 3. The graphs represent the average percentage of spore viability for a given month. It will be noted that during October there was a relatively high percentage of viable urediniospores for the years of 1935, 1936, and 1937. The germination tests showed from eighty-five to ninety-five per cent of the spores viable. For November of the different years the viability varied from forty per cent to seventy-five per cent. For the remaining winter months there was still greater variation in urediniospore viability. In December of 1935, twenty-five per cent of the urediniospores were viable while none germinated in January. In December and January of 1936-37, thirty per cent and five per cent germination was obtained, respectively, while in February the results were negative. In December of 1937, ten per cent of the spores were viable, while none germinated the following months. During the three winters in which germination tests were made, no viable urediniospores were found after the month of January.

The meteorological data, for the period covered by this investigation, may help to explain the seasonal differences in urediniospore viability. Lambert (4) reported that at San Antonio, Texas, where urediniospore overwintering has been found to occur, the daily mean temperature

is frequently above 65°F. during each month of the winter. At Dallas, Texas, where no evidence of urediniospore overwintering has been found, the daily mean temperature was never above 65°F. The graphs, showing the daily mean temperature during October, November, and December of 1935, 1936, and 1937 for the Greensboro, North Carolina, area, are shown in figure 4. The data show that October and November were the only fall and winter months during which the daily mean

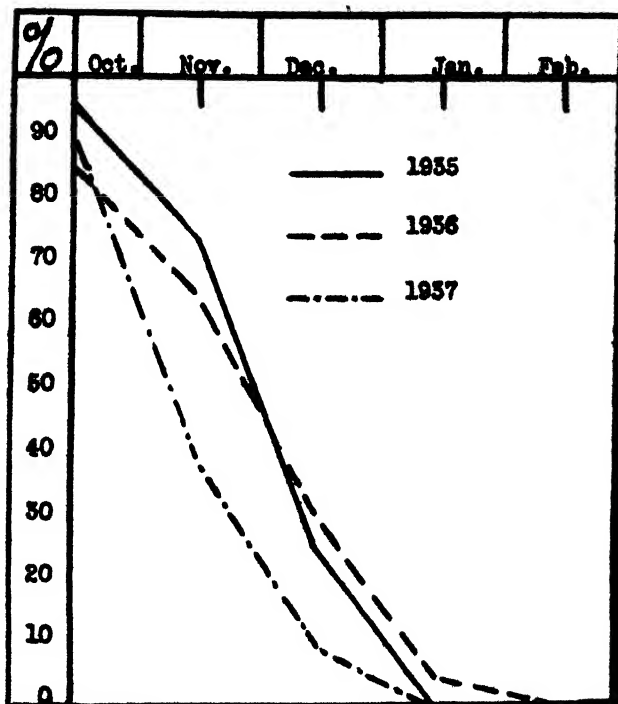


FIG. 3. Graphs showing the percentages of urediniospore viability. 1935-37

temperature was above 65°F. In fact the meteorological records reveal that the daily mean temperature was seldom above 65°F. from November to May. If there must be several periods in each winter month during which the daily mean temperature is above 65°F., in order that new uredinial infections may take place, then the meteorological records may help to explain the differences found in urediniospore viability.

Upon referring again to the graphs showing urediniospore viability,



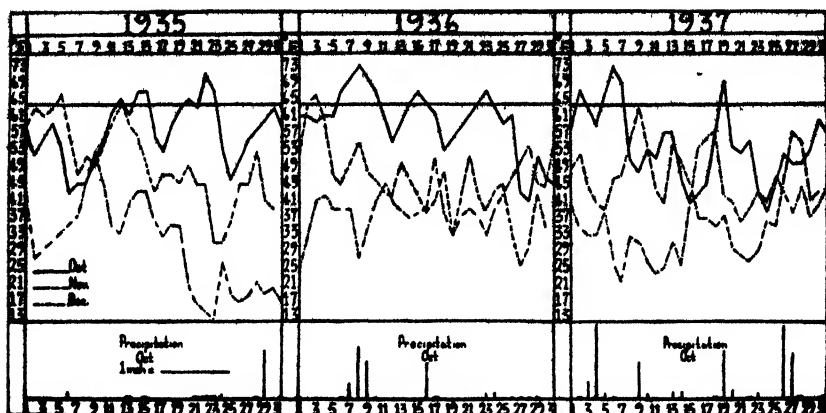


FIG. 4. Graphs showing the daily mean temperature and precipitation during October, November, and December of 1935, 1936, and 1937 for the Greensboro, North Carolina, area.

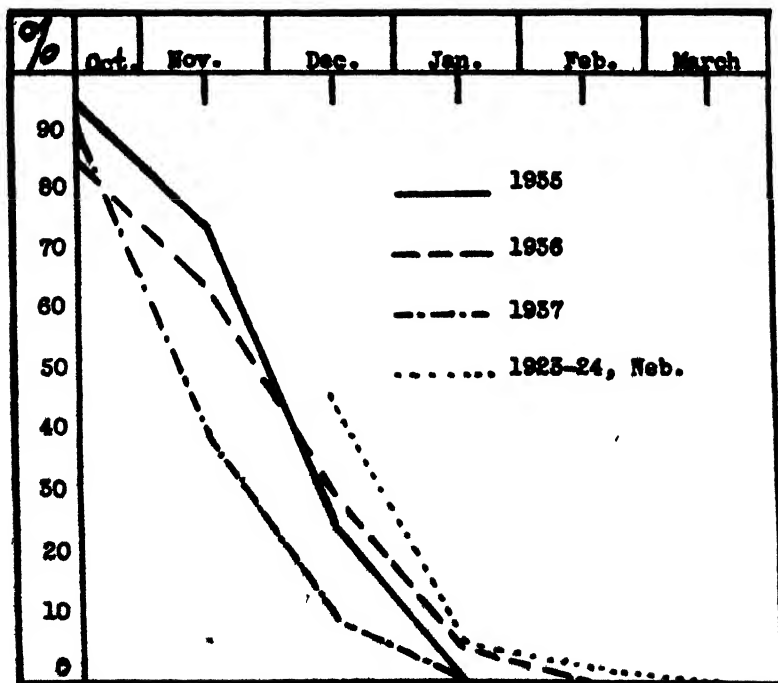


FIG. 5. Graphs showing the percentages of urediniospore viability for North Carolina, 1935-37, and Nebraska, 1923-24.

the data show a much higher percentage of viable spores during the month of December for 1935 and 1936 than for the same month in 1937. The meteorological records show three periods during October and one in November in 1935 and again in 1936 during which the daily mean temperature was above 65°F., while during November of 1937 there were no such favorable periods. These favorable temperature conditions were also accompanied with sufficient moisture for spore germination (Fig. 4). New rust infections undoubtedly took place during the first week in November of 1935 and 1936, since new uredinia were found on November 18, 1935, and on November 20, 1936. It was the spores from these new uredinia, formed during November, which showed a relatively high percentage of viability during December and January. During November of 1937, on the other hand, the daily mean temperature was never above 65°F. No new uredinia were found during November of that year and the germination tests for December showed only ten per cent of the urediniospores viable.

It is also interesting to compare the graphs showing urediniospore viability with one made from similar studies in Nebraska (Fig. 5). The number of viable spores for December was somewhat higher than for the same month in North Carolina, and a small percentage of spores germinated in February. Negative results, on the other hand, were obtained for this month in North Carolina. It is believed that a dry winter climate favors the longevity of the spores, whereas frequent rains followed by alternate freezing and thawing conditions are responsible for their death.

#### FIRST APPEARANCE OF STEM RUST IN THE SPRING

The wheat plants, on which uredinia were found in the fall and which were not used for the germination tests, were observed throughout the winter in order to determine their subsequent behaviour. In some cases teliospores appeared in the uredinium and replaced the urediniospores. In other cases the urediniospores were washed out of the uredinium by frequent heavy rains. Infected leaves also were killed and became separated from the plant. A few of the old uredinia could be found in March, but in April it was always impossible to find any stem rust uredinia on the leaves of their host. If any spores do retain their viability from November to May and produce new infections it should be possible to find the uredinia before the last week in May. The weather records show that the conditions are frequently favorable for uredinial infection during the later part of April and early in May.

No new infections, however, were found until the last week in May (Fig. 6). The first stem rust infections were always found earlier in Chatham and Randolph counties than in Alamance and Guilford. In certain years the new infections appear almost a week earlier in the latter counties than in the former. The date of the first appearance of stem rust in this state corresponds in general with the time of its yearly recurrence in northern Kansas.

Since the germination tests for the three winters failed to show viable urediniospores in February and March, and since it was impossible to find new uredinia in the field during April and early May, it is reasonable to conclude that the inoculum for the infections found during the last week in May did not come from overwintering urediniospores.

YEAR	COUNTIES, AND DATE OF FIRST APPEARANCE OF STEM RUST OF WHEAT
1934	Chatham, May 28. Guilford, June 2.
1935	Randolph, May 29. Alamance, June 6.
1936	Randolph, May 25. Guilford, June 1.
1937	Chatham, May 27. Guilford, May 31.

FIG. 6. Table showing the dates of the first appearance, in certain counties, of uredinia of stem rust on wheat. 1934-1937

#### SUMMARY

1. Germination tests of urediniospores were made during the three winters of 1935 to 1938. The results obtained for each year showed a high percentage of viable spores during the month of October. During November and December there was a sharp drop in urediniospore viability while in February the results were always negative.

2. The weather conditions were favorable for new uredinial infections to take place during three different periods in October of each year and during the first week of November during 1935 and 1936. Whenever such conditions prevail and inoculum is present, uredinial infections seem to take place. New uredinia on wheat were found about two weeks after such favorable periods in November of 1935 and 1936. No such favorable periods occurred in November of 1937 and no new uredinia were found in November of that year.

3. The first new infections of stem rust in the spring were always found in Chatham and Randolph counties during the first part of the last week of May while similar infections were found in Guilford and Alamance counties during the last few days of the last week in May or in the first week of June.

4. The primary source of stem rust inoculum in North Carolina does not come from overwintering urediniospores in this state. Circumstantial evidence seems to indicate that the primary inoculum in this state comes from a northward migration of urediniospores from states southwest of North Carolina where they overwinter.

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## A NEW SPECIES OF CHYTRIDIUM FROM MOUNTAIN LAKE, VIRGINIA

By J. N. COUCH

### PLATE 24

#### *Chytridium oedogonii* n. sp.

Sporangia attached to the host by a nipple-like projection, the old zoospore; usually ovoid and broadest in the distal half,  $10-17.6 \times 17-26\mu$ . Intramatrical vesicle about spherical,  $10-16\mu$  thick, giving rise to a long unbranched (usually) thread-like rhizoid,  $1.5-2.5\mu$  thick. Sporangia opening by a lid. Zoospores collecting in a ball at the tip of the sporangium,  $4-5.4\mu$  thick, uniciliate. Resting spore intramatrical, spherical or slightly flattened,  $13.4-17.6\mu$  thick, wall about  $1.2\mu$  thick, smooth; with a single large eccentric oil globule.

Collected July 1933, several times on *Oedogonium* in the lake at Mountain Lake, Virginia, where it was very abundant.

This fungus appears to be closest to *Chytridium* (= *Rhizidium*) *Schenkii* (Dang.) Scherffel. The two fungi resemble each other in the peculiar way in which the sporangium buds out from the spore instead of the latter simply enlarging to form the zoosporangium. However, in *C. Schenkii* the sporangium frequently sprouts in such a way that the old spore is pushed up to the side as shown in Scherffel's figure 127, Pl. 10 (1926a), and thus the sporangium is directly attached to the host, while in *C. oedogonii*, it is always attached indirectly to the host through the old spore. The mature sporangia are thus distinctly different in shape as will be seen by a comparison of Scherffel's figures and mine. *Chytridium Schenkii* has recently been described and illustrated by Sparrow (1933) on *Oedogonium* but Sparrow's fungus is easily distinct from the present species, as are also the seven other species described by him. *Chytridium aggregatum* Karling (1938) may easily be distinguished from the present species. In the former the sporangia, apophysis, and resting bodies are smaller and the rhizoids are much more branched than in the present species. Also in *C. aggregatum* the sporangia are quite irregular in shape, the vesicle (or apophysis) may be attached to the spore or the sporangium, and

the old spore cyst is amber to dark brown in color while in *C. oedogonii* the sporangia are ovoid or elliptic, the vesicle is always attached to the spore, and the empty spore cyst is colorless.

*Chytridium oedogonii* may readily be distinguished by the ovoid or elliptic sporangium attached to the zoospore by a narrow isthmus and by the long, very distinct and unbranched or very rarely branched rhizoids.

#### DEVELOPMENT OF THE FUNGUS

A zoospore of the parasite comes to rest on the host cell, loses its cilium and sends through the host wall a fine thread. Generally the host cell offers considerable resistance to the penetrating thread by the formation of a callus around it. Although the callus may extend over half way across the host cell, only a few instances have been observed where the growth of the fungus was actually checked by the callus. A few cases have also been observed where the longitudinal extension of the rhizoids were checked by the formation of extra wall tissue. Somewhat similar observations have been made by Scherffel (1925) and Dangeard (1937) except that in the latter's observations the host (*Closterium* sp.) was able to check the growth of the parasite (*Phlyctochytrium desmidiacearum* Dang.) by the secretion of wall material. Having gained entrance, the thread enlarges to form a vesicle, the sub-sporangial vesicle, which gives rise from its lower surface to a thread extending longitudinally through the host cell.

As development proceeds the main body of the spore which was left on the outside of the host enlarges as does also the vesicle, and the thread increases in length. This thread is remarkable in that it is comparatively very long and often straight, of nearly equal diameter throughout, and very rarely branched. Quite frequently the thread may extend through six to eight cells of the host penetrating the cross walls at the edge and apparently never through the middle part, a peculiarity probably associated with the cell wall structure of *Oedogonium*. This thread looks very little like the rhizoidal system of any of the Rhizidiaceae and its connection with the vesicle is sometimes difficult to make out, but one can be sure of its nature by following through the development from a spore and by examination with an oil or water immersion lens.

After the vesicle has reached a considerable size, the main body of the spore, which meanwhile has enlarged only slightly, but has become thicker walled, bulges out on the side. This bulge grows and finally

forms an ovoid structure which along with the remains of the spore becomes the sporangium. The nipple-like projection formed by the old spore at the base of the sporangium is very distinctive.

As the fungus grows the intramatrical bladder becomes filled with pale, glistening cytoplasm and numerous, large fat droplets. The young sporangium also contains the pale cytoplasm and fat droplets. In the thread, however, one can only observe the gleaming cytoplasm. As the sporangium matures the vesicle becomes empty, a process which appears to take place slowly since I have been unable to observe any rapid flow of material from the vesicle into the sporangium.

The large droplets now undergo digestion so that the protoplasm has a more or less evenly granular appearance. Small granules flow together to form larger ones until there is a single large globule of fatty substance for each spore. Spore formation appears to take place in the same way as has been described for *Rhizophidium* and other genera.

A circular lid is formed at the end of the zoosporangium and when the latter opens by the swelling of the spores, the lid is suddenly pushed to one side. The spores come out and collect in a smooth spherical mass at the mouth of the sporangium as though held by a gelatine bubble. In all sporangia in which I have observed the act of spore discharge a few spores remained within the sporangium after the main mass had been extruded. The spores remain quiet at the sporangial mouth for about two minutes after emergence. Then slowly the outer ones begin to separate a slight distance from the mass and soon the entire group spreads out. The spores now begin to show autonomous motion and in a few seconds they have all darted away. The spores left in the sporangium may creep out by amoeboid motion. Sometimes it may take such spores thirty minutes to find their way out. Scherffel (1926a) states for *Chytridium Schenkii* that apparently the formation of the cilia takes place during the resting period while the spores are at the tip of the sporangium. From my own observations, however, it appears that the cilia are already formed when the spores emerge, and that each cilium is wrapped around the body of its spore. When the spores begin separating from each other, one can observe the cilia uncoil and slowly straighten out. I have also observed this condition in *Rhizophidium carpophilum* and several other chytrids. The zoospores are rather large, uniciliate, and swim by the darting and hopping motion as is characteristic for the chytrid spore.

The resting spores are formed intramatrically. The zoospore cyst remains as an empty bladder and the resting spore is formed within

the vesicle. When mature it is covered by a rather thick membrane and contains a large fat globule partly surrounded by smaller granules and protoplasm. The germination of the resting sporangia has not been observed.

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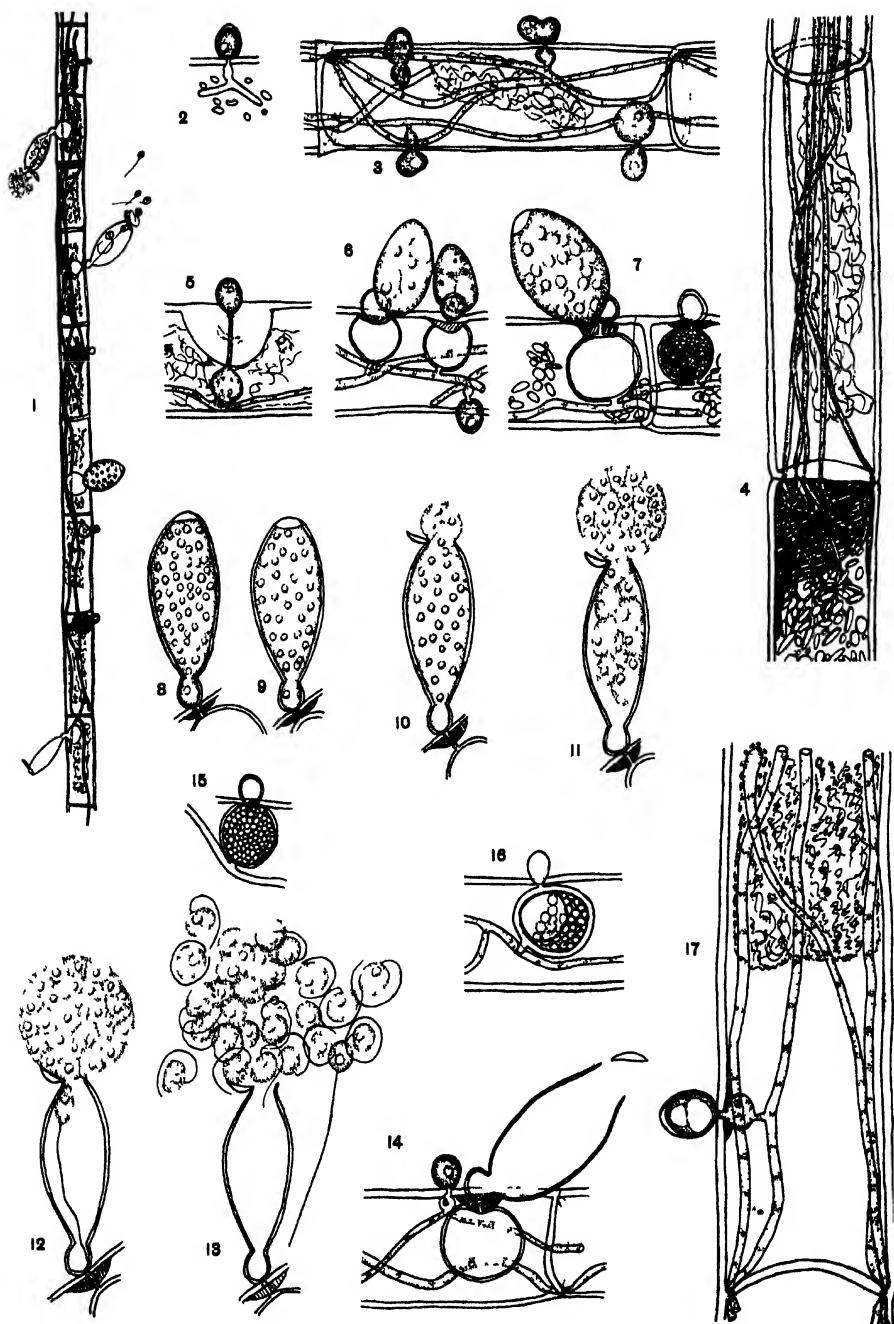
#### EXPLANATION OF PLATE 24

1. Sketch showing threads of parasite extending through several cells of host, sporangia, spores, and resting bodies.  $\times 236$ .
2. Spore germination and an early stage in the formation of hypha and apophysis.  $\times 836$ .
3. Early stages showing two young sporangia budding out from sides of spores. The two other spores are apparently destined to form resting bodies.  $\times 836$ .
4. Threads extending through cell walls, one of which has laid down a thick callus through which threads have penetrated.  $\times 836$ .
5. Spore with very long germ tube penetrating callus.  $\times 836$ .
- 6, 7. Sporangia of different ages and one resting body to right.  $\times 836$ .
- 8-13. Stages in emergence of spores. 13 shows cilia uncoiling.  $\times 836$ .
14. Empty sporangium showing old spore, apophysis and discarded lid; also note young thallus.  $\times 836$ .
- 15, 16. Nearly mature and mature resting bodies.  $\times 836$ .
17. Young thallus showing contents, also showing one of threads with a swollen end.  $\times 1400$ .





# PLATE 24





## NOTES ON AGARICS FROM TENNESSEE AND NORTH CAROLINA<sup>1</sup>

By ALEXANDER H. SMITH and L. R. HESLER

### PLATES 25-26 AND ONE TEXT FIGURE

While collecting in the Great Smoky Mountains National Park and also at Highlands, North Carolina, during the early part of September, 1937, the writers found a number of species which were particularly interesting because of extended distribution or because of insufficient information about them in the existing literature on North American agarics. Ten of these are included in this paper.

During October, November, and December of 1937 the senior author, with the aid of a grant from the Horace H. Rackham School of Graduate Studies of the University of Michigan, collected extensively along the northern coast of California and into southern Oregon as well as on the western slope of the Cascade Mts. in Oregon near McKenzie Pass. Certain discoveries were made on this expedition which were exceptionally interesting in view of the material collected in the south during early September. The discovery of *Amanitopsis farinosa* (Schw.) Atk. growing in great abundance under a dense spruce stand near Smith River, Calif. was outstanding. The distribution of *Collybia nitellina* (Fr.) Quél. has been extended in North America from Ontario south to Mt. LeConte in Tennessee, and west to the Siskiyou National Forest in northern California. *Hygrophorus ovinus* Fr. has been found in northern California and also on Mt. LeConte in Tennessee. *Inocybe fuscodisca* (Pk.) Massee was collected under redwood in northern California and under pine at Highlands, North Carolina. *Lepiota roseifolia* Murrill, a supposedly western species, which was very abundant in the western conifer forests during the 1937 season, was collected in a mixed forest near Elkmont, Tenn., in September. The presence of these unusual species in both areas indicates that their mycofloras have many more elements in common than has been believed previously, and emphasizes the need for continued critical studies in both areas.

Specimens from the collections cited jointly have been deposited in both the Herbarium of the University of Michigan and the Herba-

<sup>1</sup> Papers from the Herbarium of the University of Michigan and Contributions from the Botanical Laboratory, The University of Tennessee, N. Ser. 29.

rium of the University of Tennessee whenever the material was divisible. All other collections cited have been deposited in the Herbarium of the University of Michigan. The color names in quotation marks are taken from R. Ridgway, Color Standards and Nomenclature, 1912.

*Amanitopsis farinosa* (Schw.) Atk. This species was collected on several occasions in the Great Smoky Mountains National Park, both in Tennessee and North Carolina and also at Highlands during September, 1937. Hesler (4) and Coker (2) report it as being rather rare. During November the senior author collected it in abundance under spruce at Smith River, Calif. (A. H. Smith #8753, Nov. 16, and #8882, Nov. 19). Since the species has generally been regarded as native of southeastern United States its abundance in northern California is of exceptional interest.

*Collybia nitellina* (Fr.) Quél. *Pileus* 2-3 cm. broad, convex to plane or the margin uplifted and wavy, glabrous, somewhat moist, subhygrophanous, margin becoming striatulate at maturity, evenly "orange-cinnamon" to "pinkish cinnamon," fading slowly to near "cinnamon-buff," *flesh* thin but firm, pallid or tinged like the pileus, odor and taste mild; *lamellae* close, adnate with a tooth or subdecurrent, narrow to moderately broad, near "vinaceous-buff" or with a stronger incarnate tinge, edge even, occasionally staining faintly yellowish when bruised; *stipe* 2-4 cm. x 2-4 mm., equal, often compressed, hollow, concolorous with the pileus, sometimes paler, fragile; *spores* 6-7 x 5-6  $\mu$ , broadly ellipsoid, hyaline under the microscope, dull pinkish in mass, hyaline to faintly yellowish in iodine, with a wrinkled outer wall; *pileus trama* homogeneous; *cheilocystidia* and *pleurocystidia* not differentiated.

Gregarious to subcespitose under beech and hemlock, Mt. LeConte, Great Smoky Mountains National Park, Tennessee, Sept. 6, 1937, Hesler and Smith #7455. It was found by the senior author, Smith (11), at Lake Timagami, Ont., and recently collected in the Siskiyou National Forest, California (Smith #8323). This species and *Collybia sublatericia* Murrill are very similar. The smooth spores and strong taste of the latter distinguish it, however. The determination of *Collybia nitellina* in North America is complicated by the existence of two other orange Collybias, one of which has echinulate spores which are white in mass, and the other with smooth white spores and an hygrophanous "Kaiser brown" to "ferruginous" pileus, "hazel" gills and no distinctive odor or taste. Our data at present are insufficient to warrant a specific disposition of these.

*Hygrophorus ovinus* Fr. *Pileus* 3.5-4 cm. broad, convex to hemispheric, becoming broadly convex to somewhat expanded in age, brownish fuliginous at first or near "clay color" to "pinkish buff," paler and more grayish when faded, moist and scarcely subviscid, soon dry and minutely fibrillose squamulose, margin somewhat rimose in age; *flesh* thick on the disk, thin toward the margin, pallid to whitish, soon reddish when cut or bruised, odor faint or pronounced, pungent, taste slightly unpleasant; *lamellae* whitish, readily staining pinkish when bruised and finally spotted blackish, becoming blackened when dried, adnate at first, becoming deeply emarginate, broad, moderately close to subdistant; *stipe* 2-5 cm. x 4-10 mm., equal, not tapered below, hollow, usually somewhat compressed and sometimes furrowed, readily becoming pinkish or vinaceous where handled or bruised and finally blackish, concolorous with the pileus or paler; *spores* 7-9 x 5-6  $\mu$ , ellipsoid; *basidia* four-spored; *pileus trama* homogeneous, no true gelatinous pellicle present; *gill trama* parallel to subparallel.

On a gravel bank, Mt. LeConte, Great Smoky Mountains National Park, Tenn., Sept. 6, 1937, Hesler and Smith #7457. At Prairie Creek State Park, Orick, Calif., Dec. 4, 1937 (Smith #9392), under mixed pine and young redwood. The sharp odor, equal stipe, changing flesh and gills, and deeply emarginate gills distinguish our collections. As Kühner (7) has pointed out, the gill trama more closely resembles that of species in *Hygrocybe* than in *Camarophyllus*. Konrad & Maublanc (6) consider *Hygrophorus metapodius* Fr. as a synonym of the above species. The specimens cited here are intermediate between the two species as described and illustrated by Bresadola (1). There has previously been considerable doubt as to the occurrence of either one of these species in North America.

*Hygrophorus Peckianus* Howe. *Pileus* 15-25 mm. broad, convex, becoming more or less expanded and with a slightly depressed disk in age, glabrous, appearing somewhat canescent, hygrophanous, "snuff brown" over all when moist, fading to a sordid ashy gray, margin thin and even; *flesh* pallid, moderately thin, soft, odor and taste mild; *lamellae* broadly adnate at first, becoming decurrent, triangular, distant, broad, concolorous with the pileus; *stipe* 5-8 cm. x 4-7 mm. at the apex, 2-3 mm. at the base, concolorous with the pileus, dry, hollow, faintly fibrillose, glabrescent; *spores* 4-5 x 4  $\mu$ , globose to subglobose, hyaline, smooth; *basidia* 34-42 x 5-6  $\mu$ , four-spored; *gill trama* of interwoven hyphae.

On humus, deciduous woods, Indian Creek, Great Smoky Mountains

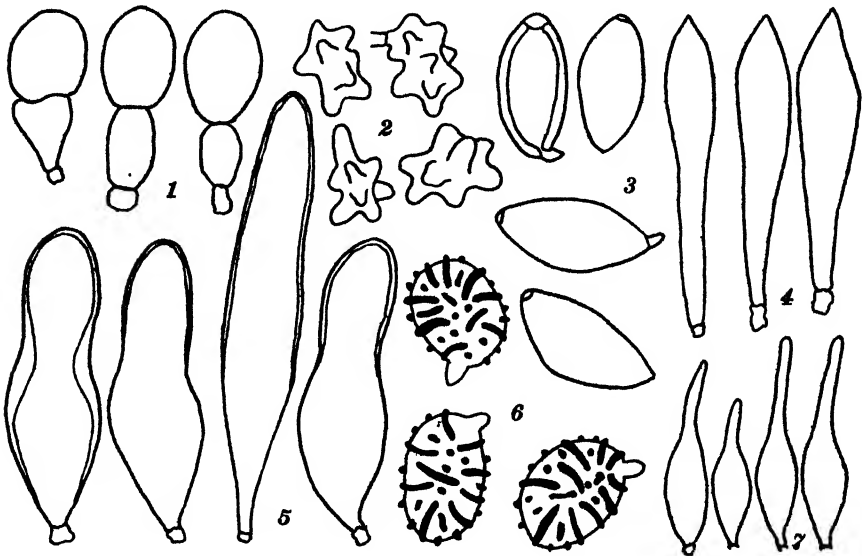
National Park, North Carolina, Sept. 5, 1937, Hesler and Smith #7397. Although the fruiting bodies of this collection possessed smooth spores and lacked a distinctive odor they undoubtedly belong here. In water mounts of fresh material the spores appeared rough under a 3 mm. objective. However, when stained and studied under an oil immersion lens they were seen to be smooth. Material of this species at the New York Botanical Gardens, collected by Morris in Massachusetts, has spores identical with those of our collection. The absence of the characteristic odor may indicate that in this species, as in others such as *Armillaria caligata* Vitt., Smith (12), odorless and odorous forms occur.

*Inocybe fuscodisca* (Pk.) Massee. (Pl. 25, top). *Pileus* 1-2.5 cm. broad, obtusely conic, campanulate or expanded and with a conic umbo, disk "mummy brown," margin paler and ashy brown, more or less virgate with appressed agglutinated fibrils, subviscid, margin subrimose; *flesh* white, thick on the disk, tapering to the margin, odor disagreeable, taste mild; *lamellae* adnate, moderately close, broad, equal, white, becoming "tawny-olive," edge white-floccose; *stipe* 4-7 cm. x 2-3 mm., equal or slightly enlarged below, stuffed, appressed fibrillose, apex pruinose, whitish from the fibrillose covering, glabrescent and grayish in age; *spores* 7-9 (10) x 4.5-6  $\mu$ , smooth, ellipsoid, furnished with a hyaline apiculus; *pleurocystidia* and *cheilocystidia* similar, abundant, 40-60 x 10-20  $\mu$ , smooth, midportion greatly inflated; neck 8-10  $\mu$  wide, apex obtuse and frequently incrustated; *pileus trama* with a layer of matted slender hyphae over the surface, the remainder homogeneous, no typical gelatinous pellicle present.

Gregarious under pine, Highlands, North Carolina, Sept. 10, 1937, Hesler and Smith #7530. The matted fibrils forming the surface layer of the pileus tend to separate from the flesh as well as from each other near the margin, leaving the white flesh exposed in streaks or as an indefinite marginal zone. This species was collected in northern California in 1935 and again in 1937. As has been pointed out by Smith (13), the fungus is very closely related to *Inocybe virgata* Atk. In the North American Flora it was retained in *Hebeloma*.

*Inocybe tubarioides* Atk. (Text fig. 1, 2, 5; pl. 26, top). *Pileus* 1-2.5 (3) cm. broad, convex, not expanding, color evenly "natal brown" to "warm sepia" when moist, somewhat hygrophanous and fading to sordid buff, appearing glabrous to the naked eye, under a lens minutely granular-furfuraceous, neither silky nor fibrillose in age, margin faintly striate when moist; *flesh* moderately thin, watery brown,

odor and taste not distinctive; *lamellae* close, broad, bluntly adnate or subdecurrent, pallid vinaceous brown when young, sordid brownish in age and seceding at times; *stipe* 3-4 cm. x 2-3 mm., equal, solid, concolorous with the cap or with a tinge of vinaceous, often streaked with whitish silky fibrils above, sometimes longitudinally silky striate, pallid to whitish below; *spores* 7-8 x 4-5  $\mu$ , nodulose, ellipsoid in outline; *pleurocystidia* very abundant, 45-50 x 10-15  $\mu$ , obtuse, pedicel short or elongated, thin-walled or some with slightly thickened



*Inocybe tubarioides* Atk. No. 1, cheilocystidia,  $\times 800$ ; No. 2, spores,  $\times 1500$ ; No. 5, pleurocystidia,  $\times 800$ . *Lactarius lilacinus* Lasch. No. 4, pleurocystidia,  $\times 800$ ; No. 6, spores,  $\times 2000$ . *Psilocybe caerulipes* Pk. No. 3, spores  $\times 2000$ ; No. 7, cheilocystidia,  $\times 800$ .

walls; *cheilocystidia* similar, scattered to rare, the gill edges also furnished with short inflated saccate to globoid cheilocystidia.

Scattered under pine and rhododendron, Grassy Patch, Great Smoky Mountains National Park, Tenn., Sept. 3, 1937, Hesler and Smith #7355; Highlands, North Carolina, Sept. 10, 1937, #7528. Our specimens have been compared macroscopically and microscopically with specimens determined by Atkinson. The pileus appears glabrous to the naked eye, but under a lens it is as Atkinson described it. The



species is not fibrillose or scaly after the manner of most *Inocybes*, in fact one seeing the fungus fresh would not suspect such a relationship. The spores and cystidia however unquestionably place it in *Inocybe*.

*Lactarius lilacinus* Lasch. (Text fig. 4, 6; pl. 25, below). *Pileus* 3.5—6 cm. broad, plane with a decurved margin, soon becoming broadly depressed in age, often having a slight umbo and an arched margin which is sometimes crenate, surface dry, minutely innately scurfy to scaly, fibrillose under a lens near the margin, quite scaly toward the disk in age, color evenly "purple-drab" becoming vinaceous or "brownish drab"; *flesh* thin, fragile, pale vinaceous or sordid vinaceous or milk white, resembling whey, unchanging, mild or very slightly acid; *lamellae* subdistant to distant, adnate to decurrent, moderately broad, near "vinaceous buff" or with a more purplish tinge; *stipe* 3—6 cm. x 5—10 mm., equal or slightly narrowed above, solid, becoming hollow in age, dull and unpolished but not fibrillose or pubescent, "light brownish drab" or concolorous with the pileus; *spores* 6—8 x 5—6  $\mu$ , ellipsoid.

Scattered under hemlock and beech, Elkmont, Tenn., Sept. 3, 1937, Hesler and Smith #7332. Since this is apparently a very rare and poorly known species in North America, a complete diagnosis is given. Kauffman collected it at Cabin John, Md., in 1916, and determined it as *Lactarius lilacinus* Lasch. Coker (3) reported it from North Carolina under the name *Lactarius griseus* Pk. form A. Material of this form kindly lent to the writers by Dr. Coker is identical with Kauffman's collections. The colors of our collection, however, have a stronger reddish tinge than either Coker's or Kauffman's, but were more violet than those commonly described for the species in Europe. Indeed our collection might very legitimately be placed in *Lactarius spinulosus* var. *violaceus* Cke. Lange, however, has raised the question of whether *L. lilacinus* and *L. spinulosus* are distinct. Material of *L. lilacinus* received from Dr. Rolf Singer, Leningrad, U. S. S. R., is characterized by decidedly rosy colors and closer narrower gills. The spores of Dr. Singer's specimen are identical with those of ours. Not having examined abundant material, we are not in a position to comment on the range of color variation in the species. Coker (3, p. 47) describes the colors as "about light russet vinaceous or vinaceous drab of Ridgway" thus including both the rosy and bluish color forms. A careful study should be made to determine whether or not the acid taste and rosy colored pilei are characteristic of the species and whether the violet colored pilei and mild taste are characteristic of a variety.

*Lepiota roseifolia* Murrill (Pl. 26, below). Near Elkmont, Tenn.,

Sept. 3, 1937, Hesler and Smith #7330. This species was first described by Murrill (10) from California. Kauffman (5) has given a more complete description. Its outstanding character is the quick change to bright red when the cuticle of the cap or stem is bruised or broken. During the fall of 1937 the species was one of the common *Lepiotas* in the McKenzie Pass region of Oregon as well as along the coast of northern California.

*Lepiota rufescens* (Berk. & Br.) Lange. *Pileus* 1.5—2.5 cm. broad, conic to broadly convex, surface dry and covered by a dense coating of mealy pyramidal evanescent scales, evenly powdery or granular in age, margin at first appendiculate with pulverulent patches of veil tissue, whitish or sordid cream color when fresh, becoming more grayish in age and tinged reddish or dull ferruginous; *flesh* whitish, slowly rufescent where cut, fairly thick, taste bitter, odor not distinctive; *lamellae* broad, close, almost reaching the stipe, white, becoming sordid brownish when dried; *stipe* 2–4 cm. x 1.5–4 mm., white, tubular, enlarged somewhat at the base, at first covered by a dense sheath of powdery material similar to that on the pileus, becoming sordid where handled; *annulus* merely a zone of pulverulent tissue, not truly membranous, soon evanescent, whitish or sordid cream color; *pleurocystidia* scattered to rare, broadly fusoid, 25–35 x 7–12  $\mu$ , in fresh specimens filled with a granular material and arising from slender hyphae in the subhymenium which have a similar content; *spores* 4–4.5 x 2.5  $\mu$ , very minute, ellipsoid, rounded at the ends, hyaline in iodine; *pulverulence on pileus and stipe* made up of thin-walled globose cells 20–40  $\mu$  in dia.

Gregarious on humus in mixed woods, Indian Creek, Great Smoky Mountains National Park, N. C., Sept. 5, 1937, Hesler and Smith #7440, and Mt. LeConte, Tenn., Sept. 6, #7472. Because of insufficient data on species of this group in North America it seemed advisable to give a complete description of the species as we have found it. Kühner (8) describes a species with more pronounced color changes under the name *Lepiota Heiteri* Boud., and raises the question whether *L. Heiteri* and *L. rufescens* are truly distinct species. The situation is complicated in North America by the existence of *Lepiota pelasiformis* Murr. Smith has collected Murrill's species in Washington (#2983). The gills of these specimens did not darken on drying and no pleurocystidia were found. In all other respects, the specimens appear to be identical with the collections here referred to *L. rufescens*. Lange's account (9) represents our material better than any other. In his

synonymy, however, Lange includes *Lepiota rosea* Rea which is also described as much brighter colored than our specimens. It is apparent from this that a critical study of the group is necessary to clearly limit these species.

*Pailocybe caerulipes* Pk. (Text fig. 3, 7). Only one fruit-body was found, Hesler and Smith #7415, Indian Creek, Great Smoky Mountains National Park, N. C., Sept. 5, 1937. The spores of the type measure 7-9 (10) x 5-6  $\mu$ , and are furnished with a hyaline apical germ pore. The pileus is covered by a thin gelatinous pellicle made of narrow (2-4  $\mu$  dia.) radially arranged hyphae. The cheilocystidia are small but abundant (26-33 x 6-9  $\mu$ ) and narrowly fusoid. They form a conspicuous band on the gill edge. No differentiated pleurocystidia were seen. The figures have been drawn from sections made of the type, and our specimen checked in every detail with it.

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PLATE 25 .

(Above) *Inocybe fuscodisca* (Pk.) Massee. Slightly reduced.

(Below) *Lactarius lilacinus* Lasch. Slightly reduced.

PLATE 26

(Above) *Inocybe tubarioides* Atk.  $\times 1$ .

(Below) *Lepiota roseifolia* Murrill.  $\times 1$ .







PLATE 26



3



5





# THE PEDICELLATE SPECIES OF TRILLIUM FOUND IN THE SOUTHERN APPALACHIANS\*

By LANE BARKSDALE

PLATES 27-35

## HISTORICAL INTRODUCTION

The Genus *Trillium*, though known throughout temperate North America as well as in Japan, China, and eastern Siberia, probably reaches its broadest development in the Southern Appalachians of eastern United States. The present work considers only the pedicellate species of *Trillium* occurring in that region of the Appalachians which embraces southern Virginia, western North and South Carolina, northern Georgia, eastern Tennessee, and northwestern Alabama.

Since the publication of *Species Plantarum* the genus *Trillium*, as we know it today, has been in a state of taxonomic entanglement. Of Linnaeus' 3 species: *T. sessile* L., *T. erectum* L., *T. cernuum*, L., the latter, *T. cernuum*, from the beginning has been misunderstood. Today, it is generally believed that Linnaeus' name, *T. cernuum* L., referred to two plants, one of which, *T. Catesbei* Elliott, occurs only from southern Virginia to Georgia and Alabama and the other, arbitrarily known as *T. cernuum* L., occurs north of these provinces. In the light of Rendle's article of 1901 it is rather evident that Pehr Kalm collected the type for what today is known as *T. cernuum* L., the type locality of which is given as "Carolina." Kalm, however, never came to Carolina. Since further evidence, set forth in the present paper, shows that *T. cernuum* L. does not occur in Carolina, it would seem that the Linnaean name correctly belongs to what is known as *T. Catesbei* Elliott. Such a nomenclatorial change would, however, serve only to complicate further the already involved synonymy of the genus. Later on Walter, in his *Flora Caroliniana* (1788), included two species, *T. cernuum* (*T. Catesbei* Elliott) and *T. sessile* L. (*T. Underwoodii* Small), both of which are common in his home area. In 1803 Michaux treated the genus as it was then known and his interpretation of *T.*

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*rhomboideum* Michaux (*T. erectum* L.) is basically in agreement with that of the present writer, though his inclusion of *T. grandiflorum* under that head was, of course, in error. Michaux interpreted Linnaeus' *T. cernuum* to be what is now known as *T. Catesbei* Elliott and in his description he characterizes *T. cernuum* L. by its style, an organ of which the present *T. cernuum* has not the slightest vestige.

Pursh in 1814 made way for a new interpretation of *T. cernuum* L. by declaring Catesby's figures of it to be erroneous. He further described *T. cernuum* somewhat as it is known today and though he gave its range as being from "Pennsylvania to Carolina," he cited it only from the "banks of the Schuylkill river near Philadelphia." This is one of the few citations in early literature of the species as it is conceived today. Elliott (1821) described *T. Catesbei* and stated that it was "probably the original *T. cernuum* of Linnaeus." He further included *T. cernuum* in his list and noted that he had specimens "from mountains of Carolina in which the peduncles are scarcely an inch long and the petals rather larger than the leaves of the calyx." These specimens might have been plants of *T. Gleasoni* Fernald or *T. Vaseyi* var. *simile* (Gleason) comb. nov.; there is certainly little reason to believe them to have been *T. cernuum* L. since the criteria used for the identification of it were not set down until 1906. It becomes evident from the preceding discussion that the major problem in interpreting the pedicellate species of *Trillium* has mainly concerned *T. cernuum*.

Gray (1878) separated from *T. erectum*, *T. erectum declinatum*, a move which made insecure the status of *T. cernuum*, as it was then understood. Small (1903), however, did not include Gray's variety in his manual and his characterization of *T. cernuum* as it appeared in the manual was applicable to *T. erectum declinatum*.

Not until the publication in 1906 of Gleason's work on the pedunculate species of *Trillium* was much light thrown on the problem of *T. cernuum* and its affinities. Gleason raised Gray's *T. erectum declinatum* to specific rank and distinguished it from *T. cernuum* on the basis of anther-filament ratio, peduncle length plus degree of inclination, and distribution. In 1901 Harbison described several new sessile species and one pedicellate one, *T. Vaseyi*. Gleason in his work in 1906 described as *T. simile* a white form of *T. Vaseyi* Harbison and shortly thereafter House (1910) described as *T. Vaseyi* forma *album* plants which are to be identified with *T. erectum* var. *album* Pursh. Thus *T. Vaseyi* and its affinities were further complicated. Gates in 1917 wrote a taxonomic monograph of the genus in North America

in which he recognized 31 species and 9 varieties, of which 21 species and 5 varieties were wholly eastern in distribution. *Trillium Rugelii* Rendle (1901) was included in this work. Peattie in 1927 included 13 species, 2 varieties and several "formae" in his discussion of *Trillium* in North and South Carolina. In this list was included *T. cernuum* L. of which no specimens were cited. *Trillium Rugelii* was here placed under *T. erectum* var. *album* Pursh as a synonym and Rendle's description was completely misinterpreted. Small (1933) listed 10 sessile and 11 pedicellate species in his *Manual of the Southeastern Flora*. He adopted Peattie's treatment of *T. Rugelii*; listed *T. cernuum* as occurring in the Southeast; and placed the variants of both *T. erectum* and *T. erectum* var. *album* under the head of *T. erectum*. Anderson (1934) in a discussion of *Trillium* in Tennessee, mentions 7 pedicellate species among which is *T. cernuum*—included on the basis of Gattinger's citation (1901) from "Lookout Mountain, Ducktown," Tenn.

The present work, dealing only with the pedicellate members of the genus indigenous to the Southern Appalachians, admits 9 species and 3 varieties. The term "forma" is not included in the present account. Those populations which, to previous authors, have satisfied the requirements for the status of "forma" are here merely treated as noteworthy variants. The author respects the painstaking cataloguing and description of minor local variants, for only by the careful accumulations of data and listing of all such forms can the complete history of the genus be read and interpreted. However, no useful purpose is served by the formal naming of the great number of such minor variants, many of which are clearly isolated steps in a long transitional series.

This author reinstates *T. Rugelii* Rendle as a species; attempts a clarification of the taxonomic status of *T. erectum* var. *album* Pursh, and attempts to show its importance as a progenitor of the unstable *T. Gleasoni* Fernald. Furthermore, the presence of *T. Gleasoni* Fernald in the Southern Appalachians is demonstrated and proof of the absence of *T. cernuum* L. from the same area is made rather conclusive. A variety of *T. erectum* is proposed and illustrated.

#### GENERAL CRITERIA EMPLOYED IN SPECIES DELIMITATION AND INTRAGENERIC GROUP SEGREGATION

The pedicellate species of *Trillium* fall into three groups (see Plate 27) on the basis of leaf and ovary characters. The first group, generally referred to as the "*erectum* group," is distinguishable from the other

two groups in its possession of rhombic leaves and globose, six-angled ovaries (varying to flask-shaped in derived forms such as *T. Gleasoni*) with *recurved stigmata*. The second group is characterized by its elliptic to broadly ovate leaves and in its green six-angled ovaries, which in the cases of *T. Catesbei* and *T. punillum* are surmounted by a short style. The other group, which might be called the *undulatum* group, has petiolate leaves and merely three-angled ovaries.

The criteria here utilized for species segregation have been mainly those of ovary contour, though to some minor degree ovary color has been employed, and petal shape and color in some cases. In the *erectum* group species delimitation has been facilitated in some cases by the use of the anther-filament ratio as a character secondary to the ovary shape. The five species of the *erectum* group are the only species of those here considered which are really difficult to identify. They fall into two sub-groups, those with globose ovaries and those with flask-shaped ones. The species in each sub-group have been delimited on the basis of anther-filament ratio plus stamen exertion and in one case (*T. Rugelii*) on anther color.

Flower odor and pedicel inclination, both of which characters have been popular in treatments of the genus in recent years, have here been omitted or merely referred to incidentally, for each is inconstant as a specific attribute. In *T. Vaseyi*, for example, the "odor of old rose petals" is not always encountered in perfectly good specimens of the species. In *T. Catesbei* and *T. Gleasoni* the pedicels may be erect, inclined, or declined and the floral pattern of the plant still be typical of the species. A complete discussion of these invalid criteria is presented in the individual treatments of the species, following.

Any student of taxonomy when dealing with the genus *Trillium* should realize that he is confronted with an externally simple expression of the liliaceous pattern, a pattern in which, because of its utter simplicity, the slightest variation is likely to be greatly exaggerated. With this reality in mind one is better equipped to speculate upon exactly what constitutes a species of the genus *Trillium*. In the present treatment a species of *Trillium* is taken to be any interfertile population which expresses in itself and in its progeny an unique floral pattern essentially distinct from the type pattern of *Trillium* which shall arbitrarily be taken as that of *Trillium erectum*.

#### GEOGRAPHICAL DISTRIBUTION

The distribution of the pedicellate species of *Trillium* in the area included in the present work is indicated under the various species

treated. Since, however, both *T. Gleasoni* and *T. cernuum* are especially important in any consideration of the *erectum* group, some mention of their continental distribution must necessarily be made here. Accepting the Appalachians as the North-South center-line of distribution for the occurrence of *T. erectum* L. one is immediately aware of the fact that all other members of the *erectum* group occur within or on the borders of this area. In the case of *T. Gleasoni* Fernald there is a westward extension all the way from the Appalachians to the Ohio-Missouri middle regions. The Philadelphia area might be accepted as the locality of greatest predominance for *T. cernuum* L. and the Ithaca region might be similarly set down with respect to *T. cernuum* var. *macranthum*. That the two species, *T. cernuum* L. and *T. Gleasoni* Fernald, interpenetrate one another's territory is evidenced by the existence of many specimens of *T. cernuum* L. for the territory of *T. Gleasoni* Fernald (Palmer, Mo. Bot. Gard. 27734, Shawano Co., Wis.) and of several specimens of *T. Gleasoni* from the area set aside for *T. cernuum* L. by Gleason (Small, NYBG Herb., Wrightsville, Penna.).

*Trillium Vaseyi* Harbison is restricted to the Southern Appalachians. Gates' citation from Connecticut was made from a specimen which should be considered to be a variant of *T. erectum* L.

*Trillium Catesbei* Elliott is more widely distributed than any other pedicellate species in the South, whereas its close relative, *T. pusillum* Michaux, is the species of most sporadic occurrence.

#### CYTOLOGICAL CONSIDERATIONS

All species of *Trillium* studied have a set of 5 pairs of chromosomes to each diploid complement. This basic genome of 10 chromosomes manifests itself in two morphologically distinct patterns each of which is peculiar to one of the two subgroups of the genus: i.e., (1) the sessile species and (2) the pedicellate species. The major difference in the ideograms of these two groups is in the configuration of the I-chromosome which is characterized (1) in the sessile species by a subterminal constriction with a knob-shaped or spherical minor element and (2) in the pedicellate species by a subterminal constriction in which the shorter arm is hooked back upon the longer arm in such a manner as to suggest a shepherd's staff.

Photomicrographs, drawings, and permanent mounts of the complements of many of the sessile and all of the pedicellate species were obtained by the present writer from smears made in the field through the use of modifications of the McClintock method. Of the pedicellate

species, the *erectum* group offers the greatest difficulty in species delimitation. The cytological considerations here set forth are concerned solely with that group.

During the course of examination of several hundred root tip smears the following scheme of designating the various member-pairs of the complement was adopted as being the most practical. This designation scheme is followed consistently in all the species. The identification of member-pairs is, in some cases, very difficult and fraught with danger. The author, as a result of extensive observations, has reason to believe that, at least in one instance, in a recent paper on this matter, misidentification of certain member-pairs has been made. It is primarily to avoid such confusion that designation-schemes of former workers in *Trillium* are rejected in favor of the present one.

The general complement of the pedicellate species is made up of five member-pairs which are conveniently designated here as pair-I, -II, -III, -IV, and -V. The two I-chromosomes of the set are characterized by a subterminal constriction so formed as to make the short arm appear crooked back upon the long arm somewhat like the crook on a shepherd's staff. The II- and III-chromosomes are possessed of median to slightly submedian constrictions which give to them the so-called V-shaped appearance. The II-chromosomes are distinguishable from the III-chromosomes by their longer and more equal arms. The IV-chromosomes are easily recognized by their L-shape which results from a submedian constriction in which the long arm is from two to two and one-half times as long as the short arm. The V-chromosomes contain more chromatic material than any other member-pair of the set. They are medianly constricted and consequently V-shaped.

The following taxonomic analyses of the species of the *erectum* group have been made from differences detected in the examination and subsequent comparison of the genomes of the respective species.

*T. ERECTUM*: I-chromosome typical of the pedicellate species; II- and III-chromosomes more bulky than in other members of the *erectum* group, the II-chromosome of the upper row is possessed of a distinctly enlarged long arm; IV-chromosome of the lower row has a proportionately shorter minor element than do any of the other members of the *erectum* group; V-chromosome typical of the group. (Plate 29, no. 1.)

*T. ERECTUM* var. *SULCATUM*: I-chromosome typical; II-chromosome distinctly larger than in *T. erectum*; III-chromosome arm ratios slightly

differing from those of the preceding species; IV-chromosome of the top row characterized by a longer minor element than in *T. erectum*; V-chromosome typical of the group. (Plate 29, no. 3.)

*T. ERECTUM* var. *ALBUM*: Because the ideograms of *T. erectum* and *T. erectum* var. *album* appear to be essentially the same when taken at the same stage, the ideogram of *T. erectum* var. *album* illustrated in plate 3 was taken from another stage (early anaphase figure in contrast to the late anaphase stages from which the ideograms of the other species here considered have been taken) in an effort to show the variation possible in the same complement when seen at different stages. It will be noted that there is considerable compactness to the I-chromosomes and that the short arms of the I-chromosomes appear to be possessed of more chromatin than they do in the ideogram of *T. erectum*. The II-chromosomes appear to be at a more advanced stage than do the I-ones; their arm ratios are slightly at variance with the same member-pair of *T. erectum* (Plate 29, fig. 1). The III-chromosomes, as well as the IV- and the V-ones, are alike, except for size, the corresponding member-pairs in the complement of *T. erectum*. (Plate 29, fig. 2.)

*T. GLEASONI*: I-chromosome typical of the group; II-chromosomes slightly smaller than those of *T. erectum*; III-chromosome of the upper row characterized by extremely short arms; IV- and V-chromosomes similar to those of *T. erectum*. The IV-chromosome of the lower row has a short arm which is proportionately longer than the short arm of the corresponding member of the *T. erectum* complement. (Plate 29, fig. 5.)

*T. VASEYI*: All chromosomes of the *T. Vaseyi* complement are extremely large, probably the largest in the genus. The short arm in the IV-chromosome is quite distinctive and is useful as a key chromosome for the identification of the *T. Vaseyi* complement. (Plate 29, fig. 4.)

*T. RUGELII*: I-chromosome typical of the group; II- and III-chromosomes of distinct size and arm ratios; IV-chromosomes not so singular; V-chromosomes of the lower row show a striking inequality in arm lengths. (Plate 29, fig. 6.)

In recent years there have been numerous research papers in the field of cytotaxonomy and several of them have been concerned with the cytological aspects of certain species of *Trillium*. Amongst these papers have been some which attempt to establish differences between closely related species on the basis of the distinctiveness of the ideogram



of one species as contrasted with that of another. The present writer feels that such an attitude, which seems to result from the assumption that minor floral and vegetative variations peculiar to any one species will be reflected in the morphology of one or several of the chromosomes of the species complement, is, at least in the case of the genus *Trillium*, a rather naive one. In fact it would seem that workers who know how slight are the differences in the gross morphological characters between many species of *Trillium* would have adhered to the opposing assumption, that in closely related species of *Trillium* one cannot expect to see an unique variation of one of the 18 vegetative and floral parts of a *Trillium* plant reflected in the shape or size of one of the chromosomes of the complement. While the statement of such an attitude is not in accord with the descriptions which are given above relative to the ideograms pictured in Plate 29 of this paper, it is a statement which is in keeping with the present author's feeling about the value of cytological criteria for speciation in *Trillium*. The author knows from his own experience that ideograms carefully made by camera lucida from different mitotic figures of the same species of *Trillium* show differences which to some authors would be "striking." Such differences are in some cases due to the presence of artifacts and in others due to the momentary variance in the mitotic phase in which the figure was caught. This is not to say that genome variation is not important in speciation. Between distinct species there are differences which are worthy of scientific note (such as the differences between *T. Vaseyi* and *T. Rugelii* in Plate 29); but amongst species which are closely related and in which the differences are slight, care should be taken to distinguish between uniqueness of complement and mere artifactual variation in complement appearance.

#### TAXONOMIC TREATMENT

The herbaria from which the specimens are cited in this treatment are designated by the following abbreviations: NYBG, New York Botanical Garden; Mo. Bot., Missouri Botanical Garden; D, Duke University Herbarium; UNC, University of North Carolina Herbarium; GSMNP, Great Smoky Mountains National Park; and US, United States National Herbarium.

#### A KEY TO THE SPECIES

Leaves rhombic, abruptly narrowed at the tip. Ovary six-angled, not green (save in 1b).

Anthers yellow (connectives sometimes purplish).

General ovary contour globose, not flask-shaped.

Stamen equaling or only slightly exceeding the much recurved stigma tips; flowers usually erect.

Ovary maroon or dark purple.

Petals maroon.

Petals not sulcate-tipped.....1. *T. erectum*

Petals sulcate-tipped.....1a. *T. erectum* var. *sulcatum*

Petals white.....1b. *T. erectum* var. *album*

Ovary green, red, white, or white blotched with red.

Petals white, cream, green or pinkish. See variants of 1b.

Stamen much exserted beyond the slightly recurved stigma tips; flowers usually declined.

Petals maroon and imbricate (splotted in intermediates between this and the following).....2. *T. Vaseyi*

Petals white, usually imbricate.....2a. *T. Vaseyi* var. *simile*

General ovary contour flask-shaped (not globose).

Stamen equal, sub-equal, or slightly exserted beyond the stigma tips.

Anther equaling or exceeding the filament in length; pedicel merely declined

3. *T. Gleasoni*

Anther exceeded by (not equaling) the filament in length; pedicel vertically reflexed.....4. *T. cernuum*

Anthers purple.

General ovary contour globose to slightly elongate.

Anthers many times exceeding the filaments.....5. *T. Rugelii*

Leaves elliptic or ovate or elongate obtuse, not rhombic, not abruptly narrowed at the tip; ovary six-angled, green; or three-angled and sometimes creamy.

Petals all of one color: either all rose or all white.

Stigmas free to the base.....6. *T. grandiflorum*

Stigmas united into a short style.

Leaves acute-tipped.....7. *T. Catesbei*

Leaves obtuse at the tip.....8. *T. pusillum*

Petals not all one color: white with a red-purple V.

Stigmas free to the base of three-angled ovary.....9. *T. undulatum*

1. *Trillium erectum* L. Species Plantarum, p. 340. 1753.

*T. rhomboideum* Michx. Fl. Bor. Amer. 1: 215. 1803.

*T. foetidum* Salisb. Parad. Lond. 1: Pl. 35. 1805.

*T. erectum* var. *atropurpureum* Pursh, Fl. Amer. Sept. 1: 245. 1814.

*T. purpureum* Kin in Ell. Sk. 1: 430. 1817

*T. nutans* Raf. Med. Bot. 2: 99. 1830.

*T. atropurpureum* Curt. ex. Beck. Bot. N. and M. States, p. 361. 1833.

*T. erectum rubrum* Clute, Amer. Bot. 9: 76. 1905.

Plant 3 or more dm. tall; leafy bracts 8 cm. or more long, rhombic, frequently broader than long; pedicel 3 cm. or more long, erect to horizontally inclined, not declined below the horizontal leaf plane; sepals

oblong to lanceolate; petals oblong to ovate-lanceolate, frequently obtusish, maroon in color; *anthers predominantly yellow, 5 mm. or more long, rarely exceeding the ovary much in length, filaments equal or barely subequal to anthers; ovary blackish-purple, six-angled, globose with recurved stigmas.*

Type locality: Virginia.

Range: Quebec and Ontario, southward to northern Georgia.

The general feeling today amongst taxonomists interested in the genus *Trillium* that *Trillium erectum* L. is very variable is not at all unwarranted. Nevertheless to lump all these variants under one head (Small, Man. South. Fl., 1933) is a questionable move since the variants for the most part are not of the Linnean *T. erectum* but are variants of a biologically distinct unit, *T. erectum* var. *album* Pursh. For a discussion of these variations and the author's interpretation of their significance, see the following.

*Trillium erectum* in the Southern Appalachians is mostly high-mountain in distribution. It is particularly common in the Great Smoky Mountains of western North Carolina and eastern Tennessee and in the Blue Ridge of Virginia, less so in the Blue Ridge of Carolina and Georgia.

Distributional citations.—VIRGINIA. Giles Co.: *Vardell* 240. Smyth Co.: Mo. Bot. Gard. 147344. NORTH CAROLINA. Macon Co.: *Harbison* (UNC 309). Ashe Co.: *Harbison* (UNC 390). Swain Co.: *Barksdale* 515. Haywood Co.: *Barksdale* 100. Transylvania Co.: US 513262. Avery Co.: *A. Gray and party* 11782. GEORGIA. Dade Co.: US 1085037. TENNESSEE. Coffee Co.: US 959650.

1a. *Trillium erectum* var. *sulcatum* n. var.

Plant up to 6 dm. tall; leafy bracts rhombic, frequently broader than long; pedicel 4 to 12 cm. long; sepals green, incurved with sulcate tips; yellow anthers exceeding the maroon filaments; ovary subglobose, maroon with yellowish stigmas.

Type locality: Roaring Gap, Surry County, N. C. (*Barksdale*).

Range: Surry and Wilkes Counties, N. C., and probably northward into Virginia and West Virginia (Type: *Barksdale* 229, Surry Co., N. C.).

This new variety has been the source of some little disturbance in the assembling of the present work for many of its characters make it appear to be deserving of a specific rank. However, in dealing with the genus of plants in which the general pattern is so simple that the slightest variance in the expression of a character is outwardly empha-

sized, one cannot proceed too cautiously. *Trillium erectum* var. *sulcatum* is at once recognizable in the field by its ringent flowers with their maroon sulcate tips. It differs from *T. erectum* in its extraordinarily long pedicel, the general appearance of its flower, and its stamen.

Distributional citations.—NORTH CAROLINA. Surry County: *Barksdale* 229. Wilkes County: *Stewart* (B217).

1b. *Trillium erectum* var. *album* (Michx.) Pursh.

*T. rhomboideum* var. *album* Michx., Fl. Bor. Amer. 1: 215. 1803.

*T. erectum* var. *album* Pursh, Fl. Amer. Sept. 1: 245. 1814; Curt. Bot. Mag., pl. 1027. 1807, in part.

*T. album* Small, Fl. S. U. S., 1903, in part.

*T. Vaseyi* forma *album* House, Muhlenbergia 6: 73. 1910.

*T. erectum* forma *albiflorum* R. Hoffm., Proc. Bost. Soc. Nat. Hist. 36: 244. 1922.

*T. erectum* forma *viridiflorum* (Curt.) Peattie, Jour. Elisha Mitch. Sci. Soc. 42: 203. 1927.

*T. erectum* L. Small, Man. South. Fl., 1933, in part.

Plant similar to *T. erectum* L. from which it differs mainly in its white petals (rarely pinkish or green); ovary typically dark purple (in variants: green, white, pink, red, red blotched, or cream), *globose*.

Type locality: High mountains of Carolina.

Range: Quebec and Ontario southward in the mountains to northern Georgia.

This variety differs from the species only in petal color. Pursh's description of it states that the ovary is "rubro." In its present usage Pursh's name refers primarily to those plants having dark purple ovaries.

Many variations of *T. erectum* var. *album* Pursh which have got into the literature seem to be quite unworthy of a name. Such is Peattie's *T. erectum* forma *viridiflorum* which has been reputed to occur in Canada and of which Peattie says there is a "likelihood of discovering . . . this rare form . . . in mountainous Carolina." This plant does occur in the high mountains of North Carolina where the habitat is typically Canadian. The plant, however, is typical *T. erectum* var. *album* Pursh which, under climatic conditions peculiar to "late springs" and intermittent "cold snaps," sometimes has a greenish cast to its petals. Several forms of *T. erectum* var. *album* Pursh, while unworthy of designation by name, are of real evolutionary importance since they

exhibit changes in the essential organs of the flowers which suggest a development from *T. erectum* var. *album* Pursh on the one hand to *T. Gleasoni* Fernald on the other. Although in local habitat these variations are rarely associated with the unit to which their origin is attributed, their North American distribution is co-extensive with that of *T. erectum* var. *album*. They should, therefore, be regarded as sporadic offshoots of it. All of these variants which fall within the limits embraced by Pursh's variety, are characterized by *globose ovaries* (type-1 in the habitat discussions that follow). From some such offshoots, however, forms with *flask-shaped ovaries* (type-2) have developed. In turn from the plants with flask-shaped ovaries has arisen typical *Trillium Gleasoni* Fernald. For the sake of facilitating classification and at the same time keeping the number of species of *Trillium* within reasonable limits, it would be wise to regard all plants having the flask-shaped type of ovary coupled with an anther-filament ratio of 1:1 or more (with the higher digit always representing the anther) as falling within the limits of *T. Gleasoni* Fernald. Such a concept necessitates the placing of Small's *T. album* mainly under the heading of *T. Gleasoni*.

Botanists coming upon isolated specimens of these variants in the field might consider such a schematic interpretation as the foregoing of *erectum* var. *album* Pursh and its affinities to be the result of much theorizing over dried material. For isolated variants frequently appear to be "something entirely new." The conclusions set down here, however, have been drawn from observations of many colonies in the field as well as material deposited in herbaria. From a field notebook have been chosen the following three examples of colonies of variations of *T. erectum* var. *album* Pursh which illustrate all the forms as well as the inter-relationships of *T. erectum* var. *album* Pursh and *T. Gleasoni* Fernald.

I. On Hyatt Road in Swain County, N. C., there grow a number of variations which furnish types of almost every form of *T. erectum* var. *album* as yet described. The flowers of this series have ovaries of two distinct types: (1) the globose, six-angled ovary typical of *erectum* and (2) the elongate, flask-shaped type of ovary found in *Gleasoni*. These ovary types shall be referred to respectively as "1" and "2." In the Hyatt Road colony there are plants with flowers possessing normal white petals and type-1 ovaries, the color of which varies from purple to white blotched with purple, to pure white, to cream, to greenish. There are further to be found flowers typical of *erectum album* in every

respect save that they have pink ovaries of type-2, the *Gleasoni* type. These latter plants, when they possess pinkish petals represent good specimens of Small's *T. album*, his description of which follows:

"Similar to *T. erectum* in habit, but flowers smaller: petals white or pinkish, less inclined to be acuminate, or sometimes obtuse; filaments pink or reddish: anthers often 8-11 mm. long, with pale connectives colored like the filaments: ovary pink or red: . . . In woods, N. C., Tenn., and Georgia."

*Trillium album* therefore seems to represent a point terminating a long series of variations of *T. erectum* var. *album* wherein it and all variants beyond it are to be considered affinities of *T. Gleasoni* Fernald. Small's description of *T. album* does not state that the pedicels are declined and since the description does say that the plant is similar to *T. erectum* L. it is safe to assume that the pedicels in *T. album* are erect. New York Botanical Garden specimens of *T. album* bear out this assumption. In colonies such as the Hyatt Road colony there are plants which agree in detail with *T. album* save that the pedicels are declined. Such plants fit the description given by Gleason for his *T. declinatum* (now *T. Gleasoni* Fernald). Thus it is evident that certain variational extremes of *Trillium erectum* var. *album* Pursh are what Gray called *T. erectum* var. *declinatum*, what Gleason called *T. declinatum* and what Fernald has since called *T. Gleasoni*. In segregating *T. erectum* var. *album* Pursh from *T. Gleasoni* Fernald one must consider two types of differences: (1) those which belong to the extreme units of each species and (2) those which are peculiar to the transitional units. Considering the characters of the "extremes" it can be seen that *erectum* var. *album* has erect white flowers with globose dark purple ovaries with stigmas much recurved and anthers on straw colored filaments which are not much exerted; whereas *Gleasoni* possesses declined white-pinkish flowers with flask-shaped ovaries whose stigmas are not much recurved and whose stamens are sometimes much exerted with pinkish filaments. The major difference here seems to be the pedicel inclination and the ovary. Considering the characters of the transitional units it is seen that in *T. erectum* var. *album* ovary color varies greatly and in rare cases *plants with dark-purple ovaries may have declined flowers*, a character which is attributed to *T. Gleasoni* (GSMNP 4236); on the other hand plants having the floral characteristics of *Gleasoni* may have erect flowers (as in *T. album* Small). Thus there is sufficient evidence concerning pedicel variation in inclination to nullify *pedicel inclination* as a good specific character

for *Gleasoni*. There remain then two characters which will be of invaluable aid in separating *Gleasoni* from variants of *erectum album* and they are: (1) ovary contour (2) anther-filament ratio and stamen exertion. The latter is the more mutable of the two.

II. On Deep Creek in the Great Smoky Mountains National Park there is a colony in which the following types occur: (1) erect-flowered; petals pinkish; ovary green, globose, six-angled; stamens pinkish; (2) much as in (1) save flowers are horizontal; (3) much as in (1) save flowers are declined. In all these examples the common feature of importance is the globose ovary.

III. On Bryson Branch in the same county there is a colony of plants in which the following types occur: (1) erect flowers; petals pinkish; ovary reddish and flask-shaped, six-angled, stamens pinkish and much exerted; (2) same as (1) save the plants are smaller and the ovaries are dark purple and the flowers are declined. The common character in the Bryson Branch colony is the flask-shaped ovary. It is permissible then to assume that the Deep Creek plants are variants of *T. erectum* var. *album* Pursh and that the Bryson Branch plants are representative of *T. Gleasoni*.

Thus it is seen that *Trillium erectum* var. *album* as a taxonomic unit varies greatly within limits of coloration and pedicel inclination but not in ovary contour and further that when there is a variation in color accompanied by a parallel change in ovary contour from globose "1" to flask-shaped "2" the variation transcends the limits of *T. erectum* var. *album* and is to be classed as *Trillium Gleasoni* Fernald.

There are several specimens in the National Herbarium collected by T. G. Harbison at Sand Mtn., Ala., and labeled "*T. leucanthum* unpub." The plant is somewhat as follows: Plant about 3 dm.; leafy bracts broader than long (in the type), 5 x 6 cm.; sepals acutish, shorter than the petals; petals creamish, about 3.2 cm. long, ovate; stamen 1.5 cm. long, yellowish, filaments apparently colorless in dried material, 3 mm.; ovary 1.2 cm., pallid, flask-shaped. This plant also occurs in limited numbers in the Hyatt Road colony near Bryson City, N. C., where it was found by Mr. Burling Thomasson who called it to the attention of T. G. Harbison. In the present treatment this and the Alabama plant are regarded as variants of *T. erectum* var. *album* which fall barely in the limits of *T. Gleasoni*.

Distributional citations.—NORTH CAROLINA. Haywood Co.: *Barksdale* 252. Mitchell Co.: UNC 280. Macon Co.: *Harbison* (UNC 281). Jackson Co.: *Ashe* (UNC 282). Rutherford Co.: *Harbison* (UNC

289). TENNESSEE. Sevier Co.: *Barksdale* 402. Blount Co.: *Godfrey* B331. Knox Co.: *Jennison* (B261).

2. *Trillium Vaseyi* Harbison, Bilt. Bot. Studies 1: 24. 1901.

Plant 2 or more dm. tall; leafy bracts 8 cm. or more long, frequently broader than long, declined to cernuous, rarely otherwise; sepals lanceolate, 4 cm. or more long, acuminate; petals maroon or purple-brown, broadly ovate (rarely ovate lanceolate) and imbricate; anthers 5–20 mm. long, yellow, with purple connectives; ovary maroon, globose, much exceeded by the anthers.

Type locality: Southern Appalachians of North Carolina.

Range: Western N. C. to eastern Tenn., northern S. C., Ga., and Ala.

This *Trillium* is a very distinct species and may easily be identified by its large, declined, maroon-colored flowers with imbricated petals, as well as by its stamen which generally greatly surpasses its ovary. So far as is known *Trillium Vaseyi* does not extend northward into Virginia. It is relatively common in the Great Smoky Mountains and southwesterly in the Blue Ridge from Buncombe Co., N. C., to Fannin County, Ga., and Pickens and Oconee Counties, S. C. Though the range of *Vaseyi* is within the same political area as that of the southern limits of *erectum* it is important to note that it grows mainly in the lower altitudes, whereas *erectum* is mainly restricted to boreal regions of the high mountains.

A discussion of the variations of this species is included under the following.

Distributional citations.—NORTH CAROLINA. Haywood Co.: *Barksdale* 219. Transylvania Co.: *Barksdale* 231. Swain Co.: *Barksdale* 285. Macon Co.: *Harbison* (UNC 239). Jackson Co.: *Ashe* (UNC 241). Mitchell Co.: *Ashe* (UNC 242). Buncombe Co.: US 283925. TENNESSEE. Polk Co.: *Ruth* (Mo. Bot. Gard. 147343). SOUTH CAROLINA. Oconee Co.: *House* 2094. Pickens Co.: Bilt. 1135. GEORGIA. Stephens Co.: *Harbison* (UNC 245).

2a. *Trillium Vaseyi* var. *simile* (Gleason) comb. nov.

*T. simile* Gleason, Bull. Torr. Bot. Club 33: 391. 1906.

Plants much as in the foregoing except that the petals are white.

That *Trillium Vaseyi* var. *simile* is the same as *Trillium simile* is unquestionable. The author has seen Gleason's type and the sheets of the co-types and they agree in detail with material which the author



has collected over a wide area. In relation to the description of *Trillium simile* in Small (Man. South. Fl., 1933), it might be stated that almost any white-flowered *Trillium* would fit that description to some extent and that none would fit it completely.

*Trillium Vaseyi* var. *simile* grows in the company of the species, *T. Vaseyi*, as well as in isolated colonies. In colonies in which both the species and the variety occur there commonly are to be found intermediate plants which are especially peculiar as regards the ovary color. Whereas in the red and white forms of the species the ovary is maroon, in the intermediate forms the ovaries may be white, white flecked with maroon, or merely maroon, and the petals may vary from white blotched with pink to various shades of pink and pinkish purple.

Sometimes one encounters in the field colonies of *Trillium* in which some of the plants resemble *T. Vaseyi* var. *simile*, some resemble *T. Vaseyi*, while others appear to be an expression of the *Gleasoni* pattern. For the most part these peculiar variations appear to be hybrids—usually between one of the forms of *erectum album* and *Vaseyi* var. *simile*, or between *Gleasoni* and *Vaseyi* var. *simile*. The "Tryon region" plant which led Peattie to declare that *Trillium simile* Gleason did not have a declined flower is probably the product of such a cross. There follows here a set of notations from the author's field notes of a colony of *Trillium* in Swain Co., N. C., which appear to offer evidence of hybridization between the variety under discussion and *Gleasoni* or a variant of *T. erectum* var. *album* near *Gleasoni*.

Ice Plant Cove colony, Swain Co., N. C.:

(1) Plant 3.5 dm. tall; leafy bracts longer than wide, 14 x 13.5 cm.; fls. declined on an almost vertically deflected pedicel; sepals 1.2 x .9 cm., green, lanceolate; petals recurved and white, 3.5 x 1.9 cm.; anthers 9 mm. long with white filaments tinged with purple; ovary about 9 mm. to the stigma tips, subglobose; two scapes on its rhizome.

(2) Similar to "1" save for the colorless filaments and the horizontal flowers.

(3) Growing next to "2," plant stocky, 2.4 dm. tall; leafy bracts 14.5 x 16 cm., longer than broad, strongly nerved in keeping with the general stockiness of the plant; flower strikingly large, about 30° off being erect; pedicel about 3 cm.; sepals lanceolate; petals 4 x 2.8 cm., white; ovary mottled red and white, 6 mm. to stigma base, stigma recurved; anthers purplish, filaments colorless, stamen equaling pistil.

(4) Small plant, 2.3 dm. tall; leafy bracts 9.5 x 7.3 cm., longer than wide; flower horizontal beneath the leaves; petals 2.6 x 1.7 cm., maroon;

pistil 9 mm., reddish purple, of the *Vaseyi*-type; anthers exceeding pistil at this stage, being 11 mm. (further observations on this plant showed anthers to exceed pistil over a period of 3½ weeks).

(5) Similar to "1" save for a pure white ovary.

(6) Same as "4," only the ovary is white, all else, even stigmas, red.

(7) Same as "1" save flowers are horizontal beneath leaves, petals and ovary mottled red and white.

(8) Plant 4 dm. tall; leafy bracts 15–17 cm., broader than long; sepals pale green, 3.7 x 14 cm.; petals 4.7 x 3.1 cm., coriaceous, white; ovary pure white; odor similar to that of *Calycanthus*. (Odor has been mentioned in none of the preceding because according to the field notebook from which these measurements were taken there was no odor. For a discussion of the significance of odors in this genus, see the introduction.)

After observing these plants in the field for over a period of weeks during two flowering seasons the author has come to the conclusion that the entire colony of some 100 plants is the result of a cross between *T. Gleasoni* and *T. Vaseyi* or its variety, *simile*. "(1)" is nearest *T. Gleasoni* in its make-up. "(4)" represents *T. Vaseyi* in all respects save the petals which are nearer the contour of the petals of *Gleasoni*; its pistil and stamen are typical *Vaseyi*; and so on the forms may be variously interpreted in the light of the parents.

In a colony such as the above, of which there are many, a botanist is not at too great a loss for means toward solving the origin of many of the forms. However, when isolated members of such a complex are encountered there is likely to be much difficulty involved in correct identification.

#### OTHER FORMS

Near the Big Poplar in Davie County, North Carolina, there occurs a type of *Trillium* the description of which is as follows: plant 3 dm. tall; leafy bracts 10 x 11 cm., longer than broad, rhombic; pedicel 3 cm. long; sepals ovate-lanceolate, 2.5 cm.; petals white, recurved, ovate, 3 cm.; anther 6 mm., purplish, filament 5 mm., colorless; ovary globose, six-angled, white to the stigma bases which are not wholly recurved but are recurved at their tips.

Specimens of this same plant have been collected from "Forney, Cherokee Co., Ala.," by E. T. Wherry. The Davie County plant was collected by T. G. Harbison and H. R. Totten. Harbison's notes on the specimens read "*Trillium cernuum* L. . . . varies in some of its

characters from typical *T. cernuum*"; Wherry's specimen bears no extra notations but is labeled "*Trillium cernuum* L." The only character possessed by either of the sets of specimens which would suggest *Trillium cernuum* is the short pedicel, which in this author's opinion is not a good character. The present author feels that these specimens save for color much resemble his "4" in the foregoing discussion and deems it wise, until fresh material can be studied, to interpret these plants as expressions of *Trillium Vaseyi*.

Distributional citations.—NORTH CAROLINA. Graham Co.: *Barksdale* 512. Swain Co.: *Harbison* (UNC 401). Polk Co.: *Totten* (UNC 529). ALABAMA. Cherokee Co.: *Wherry* (NYBG Herb.)

3. *Trillium Gleasoni* Fernald, *Rhodora* **34**: 21. 1932.

*T. erectum* var. *declinatum* A. Gray, *Man.* ed. 5, p. 523. 1878.

*T. album* Small, *Fl. S. U. S.*, p. 278, in part. 1903.

*T. declinatum* Gleason, *Bull. Torr. Bot. Club* **33**: 389. 1906.

Plant up to 3 dm. tall; leafy bracts rhombic; pedicel erect, angled, horizontal, or declined; sepals green, acutish at the tips; petals white or pinkish-white, rarely maroon; filaments pinkish, rarely white, anthers sub-equal, equal or more commonly exceeding stigmas; ovary flask-shaped, pinkish to white.

Type locality: Ohio.

Range: Western Maryland, rarely in the Philadelphia area, and the Appalachians from Connecticut to Georgia and westerly to the middle regions of Ohio, Indiana, and Missouri.

This species is rather common in western North Carolina. It varies greatly in its flower form and is identifiable mainly by its ovary shape coupled with its petal color. The inconstancy of this species in the Southern Appalachians is no greater than in the type locality. The natural inconstancy of this species is evidenced by forms, many of which resemble *T. erectum* var. *album* Pursh and some of which resemble *T. erectum* L. The former is exemplified in specimens in the Great Smoky Mountains (*Jennison* GSMNP 4239). A full discussion of the relationships and a possible origin of this species is given under *T. erectum* var. *album* Pursh. The latter is exemplified by *T. declinatum* (Gray) Gleason forma *Walpolei* Farwell (*Friesner* UNC 300, Marion County, Indiana).

At Creve Cover Lake, Missouri, there is a large colony of *T. Gleasoni* Fernald in which there is a marked variation in the floral structure of the different plants. Some of the specimens superficially resemble

*T. Vaseyi* var. *simile* and suggest that possibly in some of its phases *T. Gleasoni* Fernald approximates an expression of a pattern closely akin to that of *T. Vaseyi* var. *simile*.

Distributional citations.—NORTH CAROLINA. Buncombe Co.: *Herbison* (UNC 279). Mitchell Co.: *Ashe* (UNC 283). Polk Co.: *Ashe* 381. Avery Co.: *Ashe* (UNC 466). Swain Co.: *Barksdale* 395.

4. *Trillium cernuum* L. *Species Plantarum*, p. 339. 1753.

?Type locality: Said to be Carolina.

Range: Probably the Atlantic seaboard from Penn. through New England.

The so-called Linnaean type of *Trillium cernuum* is reputed to have come from Carolina; yet the man who is supposed to have collected the specimen, Pehr Kalm, never came any further south than Fredericksburg, Va. Most likely Linnaeus' "Habitat in Carolina" merely referred to *T. Catesbei* which is generally conceded to have been a part of *T. cernuum* L. Many floras subsequent to the publication of *Species Plantarum* have given the southern distribution of *T. cernuum* as including Carolina. Unfortunately there are no authenticated specimens to support such an assertion. Gleason in his discussion of the territorial range of his *T. declinatum* (now *T. Gleasoni* Fernald) has arrived at the conclusion that *T. cernuum* L. is distributed over an area which "lies entirely to the north and east of that of" *T. declinatum*, but actually there is some overlapping of the territories of the two species (see under section on geographical distribution). Furthermore *T. declinatum* occurs in the Southern Appalachians, whereas *T. cernuum* does not. The author's conviction of the truth of the latter part of this statement hinges on (1) the assumption that Pehr Kalm *did* collect the specimen in the Linnean Herbarium (see Rendle) and (2) the fact that Pehr Kalm never came into either the Southern Appalachians or Carolina and (3) finally the fact that there are no good specimens from Carolina in any of the herbaria which are representative of what is known as *Trillium cernuum* L. For a discussion of some of these incorrectly labeled specimens, and even they are few, see the sections on *T. Vaseyi* var. *simile* and *T. Gleasoni* Fernald. There follows a description of the species *cernuum* gathered from observations on material which the author has had sent him from the north:

Plants 1 dm. or more tall; leafy bracts 6 cm. or more long, sometimes broader than long; sepals 1 cm. or more, not exceeding the petals; petals white, elliptic-lanceolate to ovate, 1.5 cm. or more long; anthers

equal or subequal to the filaments; ovary elongate, flask-shaped, not dark red, not maroon.

It will be noticed from this description that *T. cernuum* differs markedly from *T. erectum*, *T. erectum* var. *album*, and *T. Rugelii* in both its ovary and anther characters. From *T. Vaseyi* and *T. Vaseyi* var. *simile*, it differs primarily in its ovary character and to some extent in its stamen, though the latter is mostly a matter of relative size: the stamen being larger and more exerted in *T. Vaseyi*. From *T. Gleasoni* it differs most markedly in the anther-filament ratio: *Gleasoni* being filament 1 : anther 4 to filament 1 : anther 1, whereas in *T. cernuum* L. the ideal proportion should be filament 2 : anther 1. Other characters which seem to make it so distinct a species are for the most part intangible points which lead taxonomists to say "it's one of those things you know when you see it in the field." (A discussion of *T. cernuum* L. and illustrations of it are here included in an effort to clarify its position relative to other members of the *erectum* group.)

5. *Trillium Rugelii* Rendle, Jour. Bot. 39: 331, Pl. 426, Fig. B. 1901.

Plant 1.5 dm. or more tall; leafy bracts 6-16 cm. long, frequently broader than long, rhombic; pedicel about 3 cm. long; sepals elliptic-lanceolate, green; petals broadly elliptic to ovate, flattening from the base to the middle, then recurving, broad at the middle, white; *anther darkish purple, 3-5 times longer than the filament, connectives maroon; ovary six-angled, maroon, with much-recurved stigmas.*

Type locality: "Mountains of the Broad River, N. C."

Range: The author made three collections of this species by the Broad River in Henderson County near Bat Cave, N. C. The species seems to be restricted to Henderson and Rutherford counties, N. C.

*Trillium Rugelii* is one of the few pedicellate *Trilliums* of the Southern Appalachians which has constant enough gross morphological characters to make it easily identifiable. Upon what basis Peattie merged it with *T. erectum* var. *album* (Jour. Elisha Mitch. Sci. Soc. 44: 2, 172) and subsequently with *T. erectum* (Small, *Man. S. Fl.*, 1933) is not understood, for in no way does it remotely resemble either. Furthermore Rendle's drawing which was seen by Peattie is quite unlike either *T. erectum* or *T. erectum* var. *album*. His figure of the unique stamen of *T. Rugelii* is quite in agreement with the author's own drawing which was made from a stamen selected from an abundant supply of fresh material. The lack of latitude in Rendle's measurements is the inevitable outcome of working with dried material. Actually the plants of *T. Rugelii* vary greatly in size as do the plants of most *Trilliums*

and it can be added with considerable assurance that the size of a mature *Trillium* plant in all cases of normal development is directly proportional to the size of the root-stock, the size of which depends upon the number of years it has existed, its favorable or unfavorable location, and to a minor degree, the growing seasons of those years. In such a statement rhizomes producing more than one plant at a time are to be regarded as rhizomes producing one plant of large size.

6. *Trillium grandiflorum* (Michx.) Salisb.

*T. rhomboideum grandiflorum* Michx. Fl. Bor. Amer. 1: 216. 1800.

*T. grandiflorum* Salisb. Parad. Lond. 1: Pl. 1. 1805.

*T. erythrocarpum* Curt. Bot. Mag. Pl. 855. 1805.

*T. grandiflorum* f. *viride* Ann. Rep. Mich. Acad. Sci. 20: 157. 1918.

*T. grandiflorum* f. *roseum* Farwell. Ann. Rep. Mich. Acad. Sci. 21: 364. 1919.

Plant 2-5 dm. tall; leafy bracts 6 cm. or more long, oval or broadly oval, acuminate; peduncle 3 cm. or more long, usually erect; sepals usually imbricate, lanceolate, 2 cm. or more long; petals oblanceolate or ovate-lanceolate, white, pink, rose, rose-purple, atypically green striped or green; stamens greenish save for anthers, anthers exceeding filaments; pistil 16 mm. long with spreading stigmas.

The flowers in this species commonly open white and turn rose during the period of flowering. In the mountains of North Carolina plants of *T. grandiflorum* with flowers having green and white striped petals and with or without long-petioled leaves are sometimes encountered. These plants upon examination show themselves to be abnormal in many respects: their rootstocks frequently possess peculiar swellings and the roots do not seem to depart from the rootstock in the normal manner. Sometimes in such plants the stamen and stigma become mere curled leaflets. An examination of the somatic cells shows the chromosomes to be quite normal—at least morphologically though possibly not karyologically. Possibly some disturbance is the cause of this abnormal condition. In any event such plants should be regarded as pathological and not as representing “normal variations” or “rare forms” of the species.

The species *T. grandiflorum* in the Southern Appalachians is widespread and rather common.

Distributional citations.—VIRGINIA. Page Co.: US 400757. Bedford Co.: US 605053. Augusta Co.: Jarmin (Duke U51042). Giles Co.: Herb. Mtn. Lake Bio. Stn. Blumont Co.: House (Mo. Bot.

147327). NORTH CAROLINA. Haywood Co.: *Barksdale* 224. Polk Co.: *Peattie* 1685 $\frac{1}{2}$ . Macon Co.: *Harbison* (UNC 342). Buncombe Co.: *Ashe* (Bilt. 1236<sup>b</sup>). Ashe Co.: *Ashe* (UNC 345). Swain Co.: *Thomasson* (UNC 348). Jackson Co.: *Henry* (UNC 319). Henderson Co.: *Ashe* (UNC 346). Stokes Co.: *Barksdale* 377. TENNESSEE. Unicoi Co.: *Price* 531. Polk Co.: US 63981. Blount Co.: *Godfrey* B 333. ALABAMA. Marshall Co.: US 1698812.

7. *Trillium Catesbei* Ell. Sk. 1:429. 1817.

*T. cernuum* L. Sp. Pl. p. 339 in part. 1753.

*T. nervosum* Ell. Sk. 1:429. 1817.

*T. stylosum* Nutt. Gen. 1:239. 1818.

*T. affine* Rendle, Jour. Bot. 39:334. 1901.

Plant 2 dm. or more tall; leafy bracts 5 cm. or more long, sometimes strongly nerved, elliptic to oval, not infrequently possessing short petiole-like bases; pedicel erect, horizontal or declined, 2 cm. or more long; sepals linear, sometimes oblong, obtusish, reflexed or recurved; petals white, pink or rose, ovate, ovate-lanceolate, to spatulate, usually recurved, especially if narrow; ovary pale green, stigmas united into a style at the base.

Type locality: Pendleton County, South Carolina.

Range: Virginia to Tenn., the Carolinas, Georgia, and Alabama.

This species is very well distributed in the Southern Appalachians as well as in the adjoining piedmont. It varies greatly in size but always within limits which make it easily identifiable. It is closely related to *T. pusillum* from which it differs mostly in leaf characters. It and *T. pusillum* are the only Eastern American species of *Trillium* which have styles.

Distributional citations.—VIRGINIA. Roanoke Co.: *Pourlette* (US 608283). NORTH CAROLINA. Wilkes Co.: *Barksdale* 146. Macon Co.: *Barksdale* 148. Stokes Co.: *Barksdale* 152. Transylvania Co.: *Barksdale* 153. Buncombe Co.: Bilt. 1028<sup>b</sup>. Henderson Co.: *Campbell* (UNC 167). Polk Co.: *Peattie* 1608. Surry Co.: *Oosting* 3546. Mitchell Co.: *Drushell* 7363. Cherokee Co.: UNC 165. TENNESSEE. Blount Co.: *Godfrey* B199. GEORGIA. Twiggs Co.: US 11150. Haralson Co.: US 370936. Marion Co.: *Harper* (US 431713). Bibb Co.: *Harbison* (UNC 177). DeKalb Co.: *Pennell* (US 1582608). ALABAMA. Lee Co.: *Earle* and *Baker* (UNC 157).

8. *Trillium pusillum* Michx. Fl. Bor. Amer. 1:215. 1803.

*T. pumilum* Pursh, Fl. Amer. Sept. 245. 1814.

*T. texanum* Buckl. Proc. Acad. Sci. Phila. for 1860:443. 1861.

Plant up to 2 dm. tall; leafy bracts elliptic, 2 cm. or more long; sepals obtusish, nerved, often broader than the petals; petals purplish, obtusish, undulate margined, often merely curled; anthers and filaments about equal; pistil with a definite style.

Type locality: Carolina.

Range: Eastern Va. to S. C., Texas, and the Ozark Plateau.

There is much visual evidence which when coupled with distributional data leads one to believe that this species is a sport of *T. Catesbei*. There is a possibility that the Texan and Ozark Plateau plant, *T. texanum* Buckley, is biologically the better species, whereas *T. pusillum* may only be a derived impotent. This is merely conjectural. The author has so far been unable to secure living material of *T. pusillum* Michaux.

The only mountain specimens are from Haywood Co., N. C. The author has collected extensively in Haywood County but has not been so fortunate as to run across *T. pusillum* there.

Distributional citations.—NORTH CAROLINA. Haywood Co.: *Harbison* (UNC 595).

9. *Trillium undulatum* Willd. Ges. Naturforsch. Freunde Berlin Neue Schr. 3:422. 1801.

*T. erythrocarpum* Michx. Fl. Bor. Amer. 1:216. 1803.

*T. pictum* Pursh, Fl. Amer. Sept. 1:244. 1814.

Plant 2 dm. or more tall (where there are two on a stock frequently they are about 1 dm.); leafy bracts 6 cm. or more long, blades elliptic or ovate, having a purplish caste at time of flowering, longer than the petiole-like bases; pedicel erect; sepals lanceolate, 1 cm. or more long; petals white bearing a pink V at their bases, ovate; ovary not six-angled, merely three-parted.

This species is common in the rhododendron duff and to some extent in the balsam forests of the Blue Ridge and Smokies. It is the most distinct species of the genus in our area.

Distributional citations.—VIRGINIA. Highland Co.: US 1630610. NORTH CAROLINA. Macon Co.: *Barksdale* 226. Jackson Co.: *Ashe* (UNC 385). Transylvania Co.: *Coker* (UNC 382). Mitchell Co.: UNC 388. Haywood County: *Barksdale* 560. TENNESSEE. Blount Co.: *Godfrey* B330.

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## EXPLANATION OF PLATES

## PLATE 27

A suggested relationship scheme of the pedicellate species of Trillium.

## PLATE 28

Camera-lucida drawings of the ovaries and stamens of the species considered:

- I. *Trillium erectum*
- II. *T. erectum* var. *album*
- III. *T. Gleasoni*
- IV. *T. cernuum*
- V. *T. Catesbei*

- VI. *T. grandiflorum*
- VII. *T. Rugelii*
- VIII. *T. Vaseyi*
- IX. *T. undulatum*

## PLATE 29

Ideograms of the species of the *erectum* group.

- I. *Trillium erectum*
- II. *T. erectum* var. *album*
- III. *T. erectum* var. *sulcatum*
- IV. *T. Vaseyi*
- V. *T. Gleasoni*
- VI. *T. Rugelii*

## PLATE 30

Habit photographs:

- I. *Trillium Catesbei*
- II. *T. Gleasoni*
- III. Variant of *T. erectum* v. *album* with white ovary
- IV. *T. Rugelii*
- V. *T. erectum* var. *sulcatum*

PLATE 27

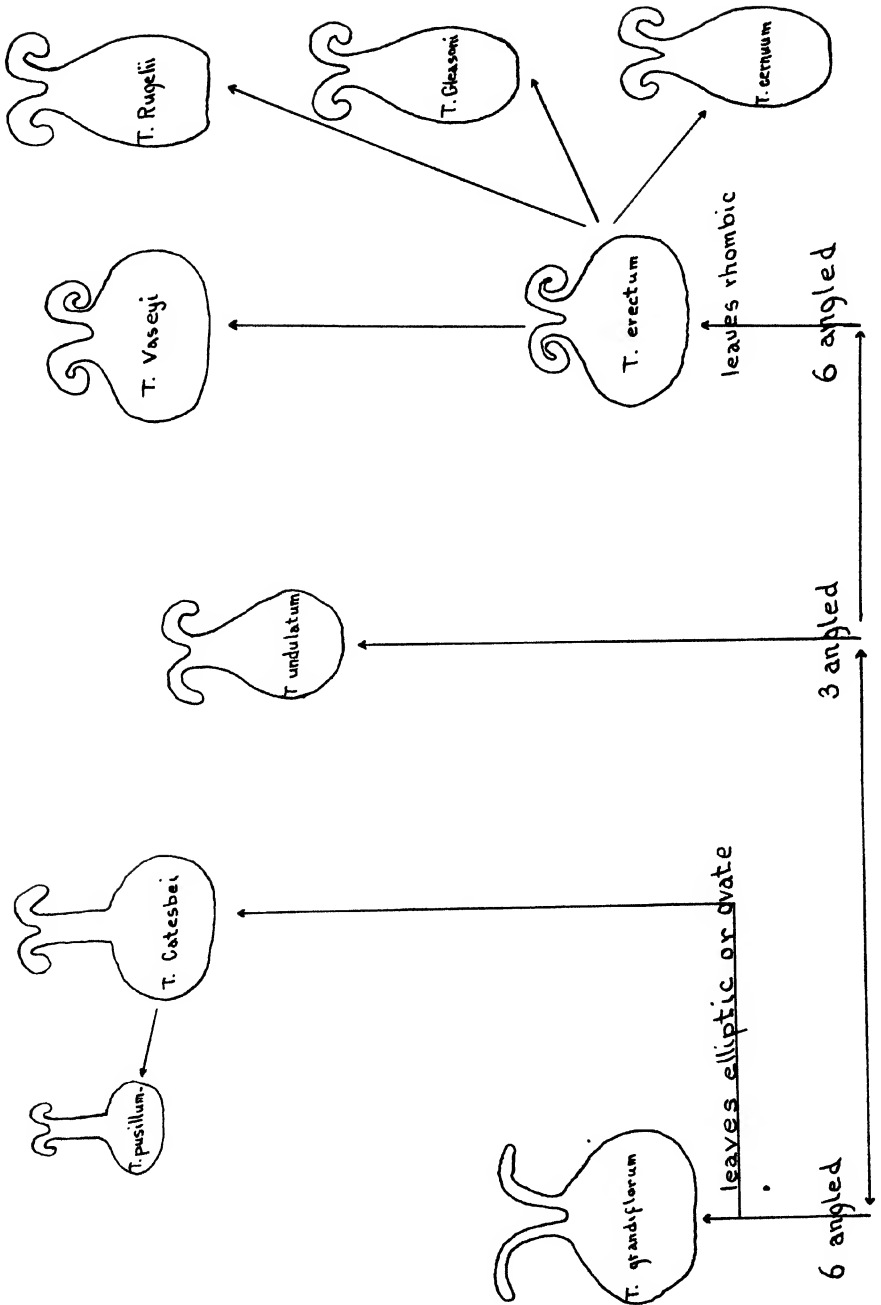
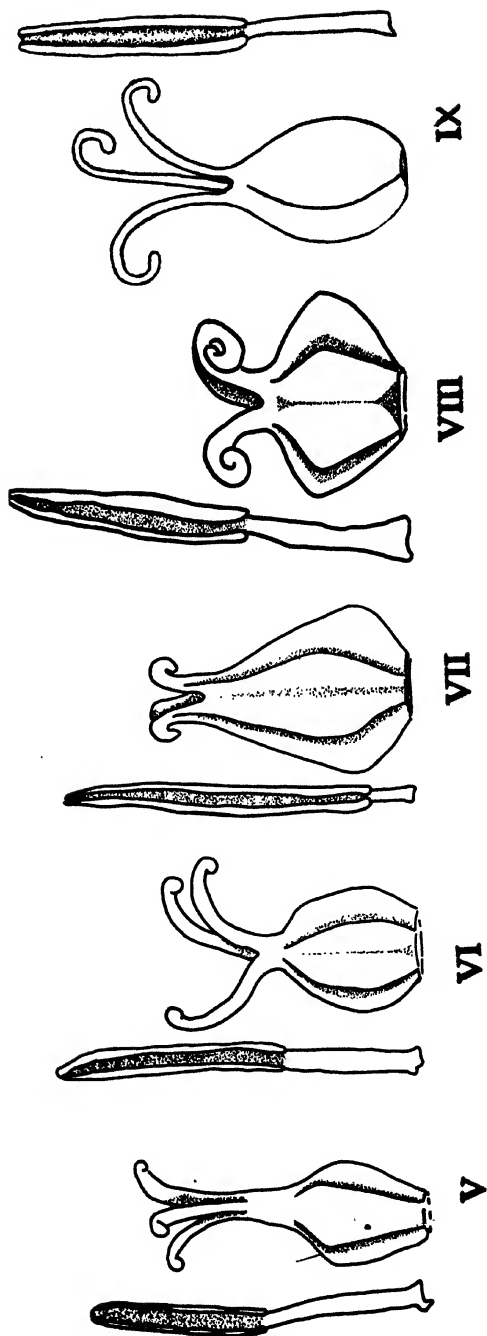
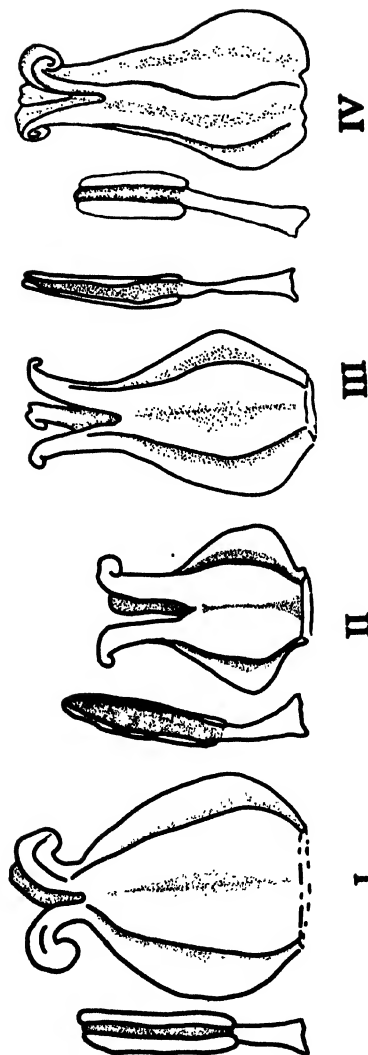




PLATE 28





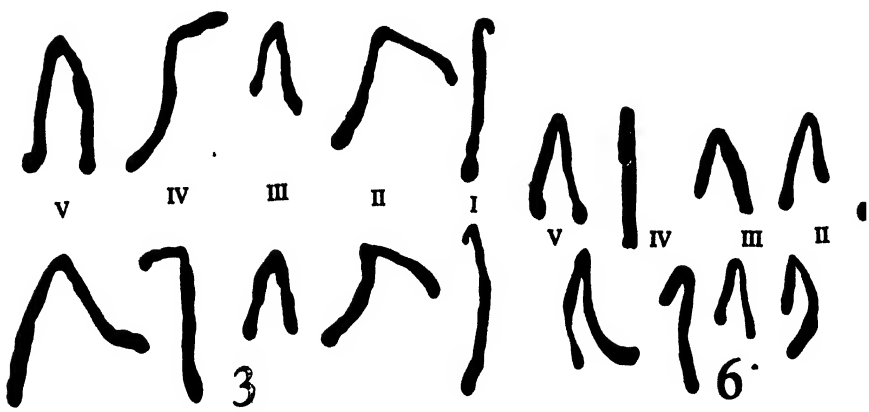
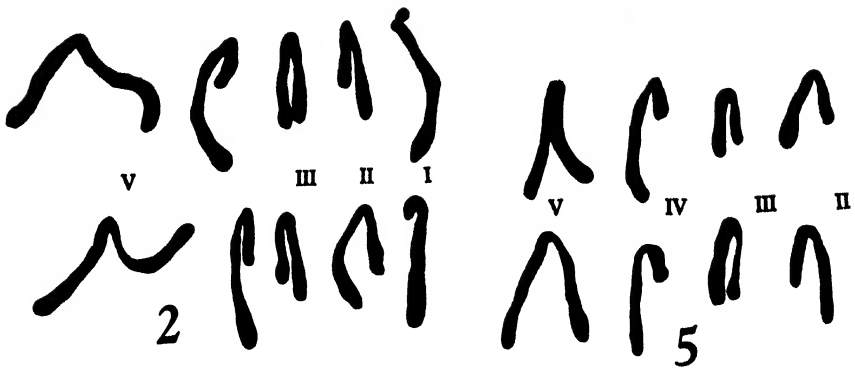
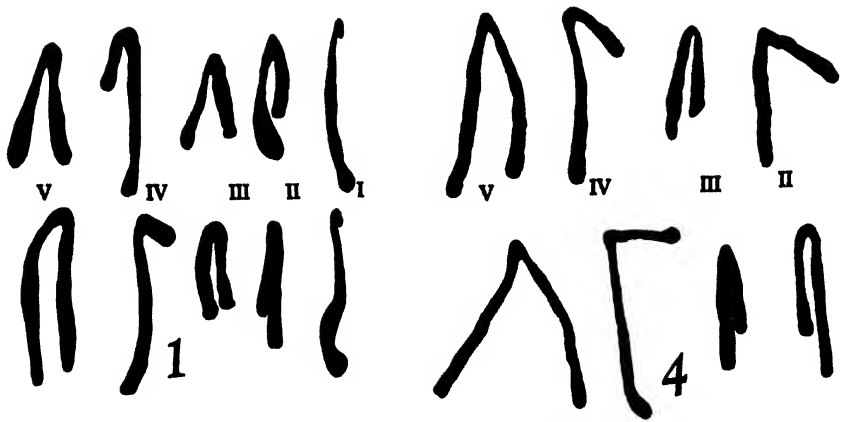






PLATE 30

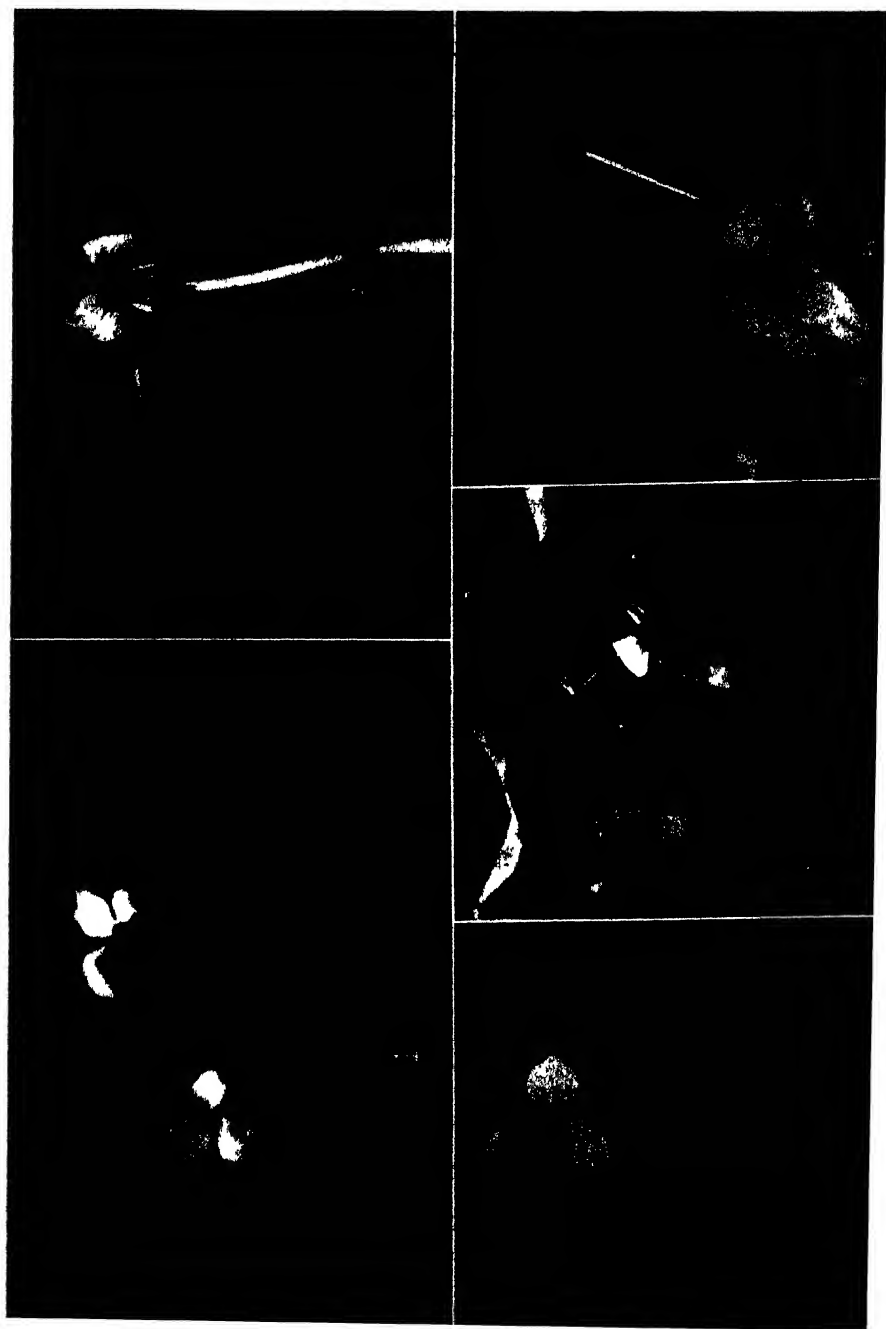




PLATE 31

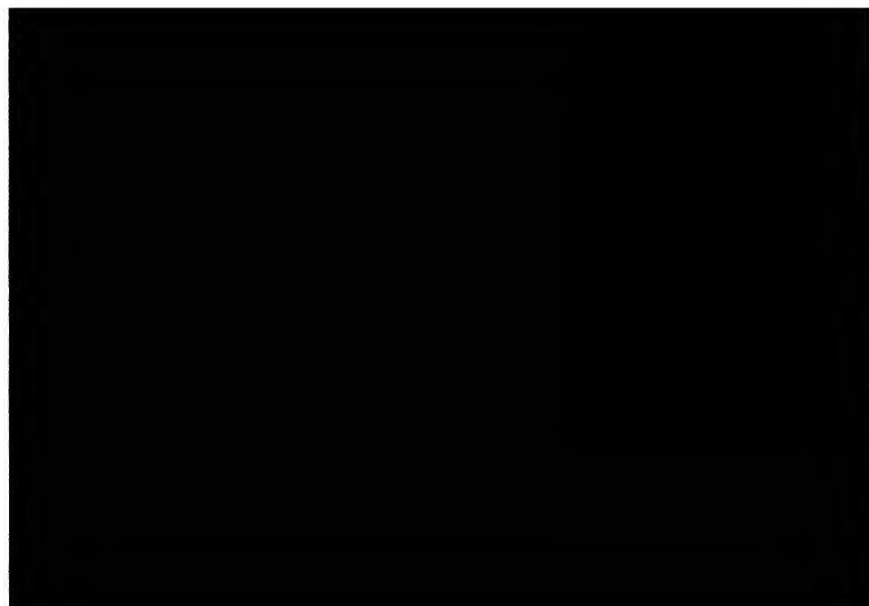




PLATE 32



T. Rugelii, Rutherford County, N. C.

T. Gleasoni, Guilford County, N. C.



PLATE 33



T. Vaseyi, habit photograph.



T. erectum var sulcatum, Wilkes County, N. C.





PLATE 34



T. Catesbei, Orange County, N. C., with nodding flower



T. Catesbei, Pilot Mt., N. C., with erect flower.







**A STUDY OF THE EFFECT OF LIGHT OF VARIOUS PERIODS  
AND WAVE LENGTHS ON THE GROWTH AND ASEQUAL  
REPRODUCTION OF CHOANEPHORA CUCURBITARUM  
(BERK. AND RAV.) THAXTER**

By **GEORGE A. CHRISTENBERRY**

**PLATES 36 AND 37**

**INTRODUCTION**

The literature dealing with the investigations of the effects of light upon the growth and development of fungi is widely scattered and covers a period from about 1821 to the present day.<sup>1</sup> The work of most of these investigators has included a variety of experiments with observations and conclusions drawn with respect to several different viewpoints. A large number of species of fungi have been used for these investigations which, in themselves, were rarely comparable. The result is that no broad generalizations can be drawn in respect to the effect of light upon the different phases of the life history of the fungi. A systematic investigation of the development of a single species in respect to its reactions to a wide variety of light conditions seemed likely to furnish some significant information. This the writer has attempted to do, and the results of such investigations are set forth in this paper.

A few papers will be mentioned which have a direct bearing upon this work. These investigations were conducted along varying lines, but they may be divided into two groups, one dealing with the effect of light on the growth of fungi, and the other with the effect of light on the fruiting of fungi.

Working on several common forms as *Mucor mucedo*, *Rhizopus nigricans*, *Sporodinia grandis*, *Cladosporium herbarum*, *Dematium pullulans*, *Pleospora herbarum*, *Neurospora sitophila*, *Fusarium* sp., *Sclerotinia trifoliorum* and *Stereum purpureum*, Weston and Hanlan (19) compiled some interesting results on the fungicidal action of ultra-

<sup>1</sup> For a more complete bibliography the reader is referred to the master's thesis of the author at the University of North Carolina for June, 1938.

violet radiation. These forms were irradiated nine minutes a day for two weeks through Petri dishes with Sanalux or Vita glass tops. A progressively reduced growth rate occurred until dormancy was reached. As the growth rate decreased, the mycelium progressed deeper into the potato agar medium. After the exposures were discontinued, the mycelial growth commenced again.

Read (16) believed that open carbon lamps emitted a higher intensity of the short fungicidal rays than did quartz-mercury lamps. Using "C" carbons at a distance of eight inches, he was able to destroy heavy infections of mature spores of *Aspergillus*, *Penicillium*, *Rhizopus*, and *Mucor* in forty-five seconds. His lamp operated on 75 amp., 60v. direct current. Smith (18) found that *Fusarium* spores were killed by an exposure of sixty seconds to a mercury arc lamp, but that temperature was important.

Much more work has been done on the effect of light and darkness, or light of various wave lengths on the reproductive activity than on vegetative vigor. In 1896 Lendner (13) worked on several different fungi, using colored filters, and alternating and continuous light. In the fungi "that have reproduction by means of sporangia," no difference in the number of sporangia was noticed on solid media, but there was a difference in the length of the sporangiophores, which were more than twice their normal length when grown in darkness or red or yellow light. On liquid media the effect of light varied according to the species, *Rhizopus nigricans* was retarded two days in the formation of its sporangia in darkness or in red or yellow light when compared with the time required to produce sporangia in white light or the violet end of the spectrum. These results did not vary with the nature of the liquid. On *Mucor racemosus*, sporangia were formed under all light conditions, but spores were not matured in darkness, very few in yellow light, and not many in red light. *M. flandus* reacted differently according to the liquid upon which it was growing. On Raulin's liquid it formed very few sporangia in white light, and none in yellow, red, or in darkness. When this liquid was made more dilute, no sporangia were formed at all, but the fungus made extreme vegetative growth. On Van Tieghem's solution, the reaction was just about opposite to that on Raulin's, sporangia being formed in greatest abundance in darkness, or in red or yellow light. *Thamnidium elegans* and *Mucor mucedo* formed their sporangia under all conditions of light on all kinds of liquids. They were formed most abundantly, however, in red and yellow light and in

darkness. Lendner concluded from his experiments that the production of sporangia was primarily a result of nutrition, and secondarily that of light.

No definite work has been done on *Choanephora cucurbitarum* with the purpose in mind of finding the effect of light and darkness, or light of different wave lengths on this fungus. Both Wolf (20) and Palm and Jochems (15) have noticed the nocturnal production of conidia. These conidia would mature on host plant organs in the early morning hours, and about noon only very scanty traces remained. The production of sporangia in nature was rare when compared with the production of conidia. Wolf performed some experiments by means of which he was able to get only sporangial formation. He concluded that light alone was not the determining factor in conidial and sporangial formation. Couch (7) noticed a marked influence of light on *C. conjuncta*. In ordinary daylight and darkness, the conidia were formed at night and matured in the early morning as in *C. cucurbitarum*, but if kept in complete darkness, conidial formation is completely inhibited.

In the selection of *C. cucurbitarum* the writer has selected, therefore, a form which seems to respond to different variations in illumination, and has carried out on this form certain experiments designed to fill up obvious gaps.

#### MATERIALS AND METHODS

*Choanephora cucurbitarum* (Berk. and Rav.) Thaxter was the fungus used in this work. It belongs to the order Mucorales and family Choanephoraceae.

The writer's description follows:

*Choanephora cucurbitarum* (Berk. and Rav.) Thaxter

Sporangia pendent, solitary, multi-spored, black, 38–160 $\mu$  in diameter; columella ovoid; sporangiophore unbranched, spores ovoid to ellipsoid, reddish-brown, smooth, 15–30 x 8–21 $\mu$ ; fine appendages terminally. Conidiophore up to 6 mm. long, smooth, terminating in a vesicle, from which arise secondary vesicles covered with conidia. Conidia ovoid, reddish-brown, longitudinally striate, 7.5–12 x 9–25 $\mu$ , short, hyaline, with basal appendage. Chlamydospore globose to ovoid-ellipsoid, walls more or less thickened. Zygosporangia bow-shaped, unequal, ovoid, 50–90 $\mu$  (zygosporangium from Wolf). Plant heterothallic.



Found on old flowers of *Hibiscus* sp., *Cucumis* sp., *Gossypium* sp., *Capsicum* sp. Found on both old flowers and young fruit of *Cucurbita pepo*, and *Solanum melongena* var. *esculentum*.

The discovery of *Solanum melongena* var. *esculentum* (egg-plant) as a new host adds another to the list which are infected by this fungus. It was collected from both flowers and young fruits as mentioned above, and got in pure culture on Blakeslee's #230 agar medium.

Many media were tried in the culture of *Choanephora cucurbitarum*; some seemed to inhibit growth and fruiting, while others, such as Blakeslee's #230, seemed to be too stimulative. When the nutritive ingredients of #230 were reduced one-half, the medium was very satisfactory, producing sporangia and conidia in approximately equal numbers, and covering a 10 cm. Petri dish in two days.

Three light-boxes were constructed for use in experimenting on the effect of light of different wave lengths on fruiting. These boxes were 11 x 5½ x 5½ inches, consisting of two equal compartments in which a Petri dish could be placed. These dishes rested on a wire rack about midway between the top and bottom in order to secure free circulation of air around the dish through the two air-vents in each end. A thermometer was placed through the top with the bulb resting level with the dish, so that the reading would be the approximate temperature of the dish. The thermometers had to be covered because they transmitted some undesired light. A hole, 1½ x 1½ inches, for the entrance of light was cut in the top of each compartment. The filters, 2 x 2 inches, were placed over the holes and held in position by wooden slots. The openings comprised the entire front of each compartment and were closed by sliding doors fitting tightly in slots. The entire box was painted black and tested for light-proofness.

Six filters were obtained from Corning Glass Works and were selected according to the portion of the spectrum transmitted. These filters are as follows:

	Transmits	
	40%	5%
#243 H. R. Signal Red.....	622μm	608μm
#348 H. R. Red Shade Yellow.....	580μm	571μm
#038 Straw Yel. Novoil Shade A.....	434μm	423μm
#306 Novoil O Shade.....	404μm	380μm
#590 Daylight.....	380μm	
#986 Red Purple Corex A. Transmits 240μm to 425μm.		

The first four filters have sharp spectral cut-offs, that is, they are practically transparent to all long wave lengths, and transmit (approx-

imately) to the shorter wave length shown in the 5% column. They were selected for this reason, each one permitting more and more of the shorter wave lengths to be transmitted. #590 was selected because it changes the color temperature of a Mazda lamp approximately to that of daylight. It cuts down on long wave lengths in such a way as to make the shorter wave lengths in the same proportion as in daylight. #986 was chosen for its ability to transmit high intensities of the short wave lengths. A maximum of over 80% is transmitted between 310-360 $\mu$  with practically none longer than 400 $\mu$ , which is at the extreme limit of the visible spectrum. It will transmit to 240 $\mu$ , but the drop is very great for those shorter than 280 $\mu$  (40%).

The light sources used were Mazda 60 W. and 100 W. bulbs. It was thought advisable to use these because their intensities would be nearly constant and easily checked. A Weston Photronic Exposure Meter Model #650 was used to regulate the intensities which were 100 foot-candles under all filters except #986. These bulbs were deficient in the portion of the spectrum transmitted by this filter, and an intensity of 8 foot-candles had to be used. Approximately one per cent of the solar spectrum is ultraviolet, therefore the writer considers this intensity comparable to the higher intensities under the other filters. The light boxes were kept in a dark room which prevented the interference of other sources of light.

The temperatures were kept within two or three degrees of each other in all the boxes so that temperature could be eliminated as a factor influencing fruiting and growth. Regulation of the air vents, the operation of fans, and the use of other lamps for heating purposes was sufficient to perform this. The temperature was kept between 30° to 35° in the light, with a decline of about 10° in the dark.

To study the effect of ultra-violet light, conidia and sporangiospores were placed on the surface of the agar in 10 cm. Petri dishes. These dishes were supported by ring stands and clamps at a distance of two inches from the source. A General Electric "Lab-Arc" mercury vapor lamp was used with filter #986 to supply the ultra-violet light. An intensity of 40 foot-candles was obtained at this distance, and the exposure periods were varied.

The method for securing the approximate number of fruiting bodies present to use in the tabulation of a graph was as follows: Twelve places were selected on each Petri dish, eight being in a circle nearly as large in diameter as the Petri dish, and four in a small circle around the point of inoculation. At each one of these positions the number of

conidiophores or sporangia present in the field of view formed by a 10x ocular and 32mm. objective were counted and recorded. A mean of these twelve counts was calculated and this taken as the number present in that experiment. An average of the means of all experiments in a series was found, and this average taken as the number present in that series. The number present in normal conditions was taken as a maximum or one hundred per cent, and the others were shown as certain percentages of this. It might be stated that under no filter in any series did the number of fruiting bodies exceed that found in normal conditions.

#### EXPERIMENTAL AND DISCUSSION

The effect of light of various periods and wave lengths on the growth of *Choanephora cucurbitarum* was not the main purpose of this work, but observations were made concurrent with those on the effect on fruiting. Light seemed to have no effect upon the linear expansion of the mycelium because in various periods of alternating light and darkness, and continuous light and continuous darkness, the mycelium was able to cover completely a 10 cm. Petri dish in about 45 hours. A difference, however, was noticed between the appearance of the mycelia exposed to different wave lengths. Wave lengths shorter than  $380\mu$  or under blue light (filters #590 and #986) caused the mycelium to have a prostrate appearance, always being less than 2 mm. high. The mycelium was more compact than that which was produced in light of wave lengths between  $571\mu$ – $380\mu$  (filters #038 and #306). The mycelium in this instance was very fluffy and loose when compared to that grown under wave lengths shorter than  $380\mu$ , and reached a height of 8–10 mm. When the fungus was grown under light between  $608$ – $571\mu$  (filter #348) the mycelium did not quite reach a height of that grown under filters #038 and #306. Under light of  $608\mu$  and longer (filter #243), the mycelium was intermediate between that grown under filters #590 and #348, not being either as flat and compact as the former, or as high and fluffy as the latter. Thus, yellow light favored a luxuriant aerial mycelium, while blue and violet light favored a prostrate mycelium. Red light lay between these two in its effect on mycelial growth. These results varied very little under different exposure periods and might be taken as constant for *Choanephora cucurbitarum*.

The effect of light of wave lengths shorter than  $400\mu$  was very marked. Filter #986, which transmits almost entirely wave lengths

between  $300\mu$  and  $375\mu$  was used in this experiment in conjunction with a mercury vapor lamp. It was found that exposures at 2 inches of different periods produced results in proportion to the length of the period. An exposure of 1 minute every twelve hours for two days had very little effect on the growth of the fungus, but with an exposure of 5 minutes noticeable effects appeared. The aerial mycelium did not extend to the edge of the petri dish, and the fungus grew mostly in the agar substratum. The growth of the mycelium was aerial in the interval between exposures, but was forced into the agar by the exposures. An exposure period of 10 minutes reduced the aerial mycelium even more, and a period of 15 minutes almost entirely eliminated the aerial mycelium even though the mycelium was abundant beneath the surface of the agar. An exposure of 25 minutes completely killed the germinating spores and conidia. No amount of raying prior to germination, however, seemed to penetrate the walls of the spores and conidia sufficient to kill them. They always germinated; only the vegetative mycelium was affected.

An experiment was conducted in order to show this effect of ultra-violet light. The conidia were placed on the surface of the agar in such a way that one half could be rayed and the other half not rayed. Exposure periods of 5, 10, 15, and 25 minutes in each twelve hours were used, and pictures taken after two days (Plate 37). Figure #1 shows the result of 5 minutes' exposure. The agar was cut from each side to prevent the mycelium from the unrayed side growing around the edges. The white line parallel with the agar strip marks the line of inoculation. (Notice in all figures.) The aerial mycelium did not reach the edge of the dish in the upper or exposed portion of the dish. Figure #2 illustrates the results of a 10-minute exposure. The difference between the upper exposed half and the lower unexposed half is even more marked. The mycelium can be observed to be very abundant under the surface of the agar, and has reached the edge of the Petri dish. Figure #3 shows the results of a 15-minute exposure. The aerial mycelium is very scanty, and the mycelium beneath the surface of the agar has not reached the periphery. Figure #4 shows a plate subjected to a raying of 25 minutes. Notice the very scant growth on the upper half of the agar. The reason that it was not entirely absent is that 12 hours is long enough for some mycelium to grow from the unrayed side, but it is killed upon raying.

Ultra-violet light appears, thus, to have an inhibitory effect on the growth of the mycelium in *Choanephora cucurbitarum*. As a result of

the raying, the fungus grows beneath the surface of the agar and is in this manner protected, the agar acting as a screen. The effect varies with the length of the exposure period, 25 minutes being sufficient to kill all hyphae that are not protected by the agar.

The effect of light of different periods and wave lengths on asexual reproduction was much more striking than the effect on growth. Under normal conditions of light and darkness, the fruiting bodies appeared on the second night after inoculation. Some appeared earlier, but the majority are formed during the second night. The conidia were more abundant than the sporangia, but both appeared together over the entire surface of the mycelium. In the early morning the conidia would not have been formed on the secondary vesicles which have a yellowish-orange appearance. At the same time the young sporangia were about the same color, the spores not having been formed. About mid-morning the conidia and sporangia would have been formed, both giving a black-speckled appearance to the mycelium. The aerial mycelium was intermediate in height, being 5 to 6 mm. high.

The study of the effect of light of different periods and wave lengths was divided into series consisting of individual experiments. The experiments of each series were as identical as possible in order that the results could be taken as conclusive. Continuous illumination was used in the first series, and in the other series the dark period was increased as the light period was decreased, until continuous darkness was used in the final series. (If continual reference is made to Plate 36, the results and conclusions will be understood more clearly.)

The production of sporangia under filter #243, which transmits red light, can be shown by a regular curve through the series. No sporangia were formed under continuous light in any of the twelve experiments performed. In series B where the cultures received one hour of darkness a few sporangia were formed in two of the four experiments, but in series C where the period of darkness was of two hours' duration no sporangia were formed at all. In series D, E, and F the number of sporangia increased steadily until a maximum was reached in series G. In each group of this series (G) the number of sporangia was large and nearly equal. This seemed to indicate that regardless of length, equal periods of light and darkness were most favorable to the production of sporangia. After series G the number of sporangia formed became gradually less. Continuous darkness was used in series J, but even in this series sporangia were formed to a limited extent, the number being approximately that formed in series D. The conclusion to be

drawn from the series under this filter is that at least 1-3 hours of darkness in every twelve is necessary for fruiting, and equal periods of light and darkness are most stimulating. However, light is not necessary for sporangial formation.

No conidiophores were formed under this filter until five hours of darkness was alternated with seven hours of light, and then only in two of the three experiments. The number of conidiophores was about the same in series G, H, and I, and reached a maximum in continuous darkness. Even here, the number was not very great, being about 1.1/f. v.<sup>2</sup> Red light did not appear to be very conducive to the formation of conidiophores since the conidiophores were very scarce in all periods of illumination and were more abundant in continuous darkness.

The maximum of fruiting occurred under filter #348 which transmitted red-yellow light. Sporangia were formed in great abundance in series A, B, C, D, E, and all three groups of series G. The numbers were approximately equal in the above mentioned series, and the drop in series F was thought to be due to the use of a new supply of agar. In series H, I, and J there was a gradual drop in the number of sporangia present, showing that this light was more favorable to fruiting than darkness. The sporangia were found under this filter in continuous light, but did not appear under any of the other filters in this series. The number of sporangia formed under this filter was not equalled under any other filter in series A through G<sub>1</sub>. The conclusion to be drawn from this is that red-yellow light does not inhibit the formation of sporangia.

The conidiophores were not formed in such great numbers as were the sporangia, but in most of the series they were more abundant under this filter than under other filters. Conidiophores appeared under this filter in series B, D, and E in small numbers, but were not found under any of the other filters. In series F, they were more abundant under both yellow filters (#038 and #306). As stated before, the conidiophores appeared in series B in small numbers. They were not found in series C, but a very few were formed in series D. The number increased greatly in series E, and except for a slight decrease in series F increased steadily in series G<sub>1</sub> and G<sub>2</sub> where a maximum was obtained. From here the drop was more or less gradual except for a slight rise in series I to series J in which many conidiophores were formed in continuous darkness. This filter had a larger number of

<sup>2</sup> f.v. = per field of view.

conidiophores formed under it than under any of the other filters except for #038 and #306 in series F, and #590 and #986 in series G<sub>2</sub>. Therefore, it may be said that this light is most favorable to the formation of conidiophores.

Likewise, the number of sporangia formed under filters #038 and #306 can be shown graphically by a regular curve. The numbers formed under these two filters were practically identical in every series with a few more being formed under #038. No sporangia were formed under continuous illumination, but a few were produced in series B which had a one-hour period of darkness. From this series the number of sporangia gradually increased through series F where many were found. A slight leveling off occurred in series G<sub>1</sub>, and then the curve reached a maximum in series G<sub>2</sub>. From here the curve decreased through series G<sub>3</sub>, H, I, and J under #038, but it had a rise in series I before dropping off to series J under #306. About 1.1 sporangia/f. v. were formed in darkness. These yellow filters have more of an inhibitive effect on sporangia-production than the two red filters.

Conidiophores were not found under filters #038 and #306 before series F, which had a five-hour dark period. Many were formed under both filters in this series with a few more under #306. This was about the maximum number formed. In series G<sub>1</sub> only a few were found, and in series G<sub>2</sub> the number present increased slightly. In series G<sub>3</sub> no conidiophores were found, but in series H and I the number increased until many were formed. Under #306 the number increased greatly, and then dropped off in darkness, but under #038 the number did not increase so much, causing a steady rise in the curve to darkness. These two filters transmit light that seems to be very inhibiting to the formation of conidiophores, because they are formed only in series which have five or more hours of continuous darkness.

Filter #590 produced results very similar to those of #038 and #306. Sporangia were formed first, as in these filters, in series B, and the increase was the same through series F except that many sporangia were formed in series C. A decline of the curve occurred in series G<sub>1</sub> similar to that found under filters #038 and #306, but the number of sporangia increased more under filter #590 in series G<sub>2</sub>. Here more sporangia were formed than under any of the other five filters. The curve dropped more rapidly through series H, a few sporangia being formed. A rise in the curve occurred in series I, which was so great that a peak was formed when it had to descend to show the number formed in darkness. The same conclusion can be

drawn for this filter as for #038 and #306 in that the rays transmitted by this filter seems to be inhibiting to the formation of sporangia.

Except for series  $G_3$ , the smallest number of conidiophores were formed under this filter. Conidiophores were formed in small numbers in series F and H and increased somewhat in series I. A subsequent drop occurred in the curve to series J. This filter also seems to be inhibiting to the production of conidiophores. At least five hours of darkness is necessary for the production of conidiophores, but under twelve hours, more are formed than under any of the other filters in all series.

Filter #986 which transmitted only the violet end of the visible spectrum and a portion of the ultra-violet spectrum had the smallest average of fruiting. Sporangia were found in very small numbers in series B, but did not appear again until series E. This series had a dark period of four hours, but even then they were in about the same number as in series B. Under all other filters sporangia were produced more or less regularly in series B to E (exception in series C of #243). From series E through J the curve of numbers present followed rather closely that of #590. The numbers increased greatly in series F, dropped in series  $G_1$  to just a few, and then the maximum number was attained in series  $G_2$ . This filter had, in series  $G_2$ , the second largest number of sporangia to be formed under any filter in any series. From this series the number decreased in series  $G_3$ , H, and I, and then increased in continuous darkness. Since sporangia are not formed in large numbers in the first five series which have long light periods, this light seems to be very inhibitive to the formation of sporangia. A long period of darkness, as in series  $G_3$ , is needed to produce sporangia.

The conidiophores formed under filter #986 were present in the same series as those formed under #590, and in about the same numbers. In series F,  $G_3$ , H, I, and J, conidiophores were formed, and except for series  $G_3$  and J were in very small numbers. In series  $G_2$  the second largest number of conidiophores formed in any series under any filter was formed under this filter. In continuous darkness (series J), the number of conidiophores present was greater than in any of the other series except  $G_3$ . This light is inhibiting to the formation of conidiophores as well as the formation of sporangia.

#### SUMMARY AND CONCLUSIONS

In this work on *Choanephora cucurbitarum* it was found that vegetative growth occurred at approximately the same rate regardless of the



light conditions. The linear expansion of the mycelium takes place at the same rate whether the fungus be kept in continuous light, continuous darkness, or varying periods of light and darkness. This is in agreement with Montagne (14), Brefeld (4), and Coons (6).

The aerial mycelium has different appearances under different wave lengths of light. Yellow light promotes a fluffy, loose aerial mycelium about 8-10 mm. high. Blue and violet light cause the aerial mycelium to be compact. In this case it lies close to the agar, being between 1 and 2 mm. high. Red and red-yellow light cause a mycelium to be formed intermediate between the previous two. This mycelium is not so high and fluffy as that under yellow light nor so flat and compact as that under blue and violet light. Ultra-violet radiation produces a remarkable effect upon the vegetative mycelium. Radiations by a mercury-vapor lamp cause the fungus to grow into the agar, the amount depending upon the length of the exposure. An exposure of 25 minutes, twice a day, was sufficient to kill germinating spores, and one of 15 minutes produced a culture with practically no aerial mycelium. This effect has been observed on *Rhizopus nigricans* and *Mucor invado* by Weston and Halnan (19) in 1930. No amount of raying seems to penetrate the spore or conidia wall sufficiently to kill the spore or conidia. It is always the vegetative mycelium which is affected. This is contrary to results obtained by Read (16) on other Zygomycetes, but Fulton (9) showed that different species have different reactions.

*Choaneophora cucurbitarum* can fruit in complete darkness, but best results are obtained when the light and dark periods are equal. Under ordinary light conditions in the laboratory, the number of sporangia and conidia produced is approximately equal. Artificial light conditions affect the production of conidia more than the production of sporangia, for there are fewer conidia than sporangia in every case except in series G<sub>2</sub>, when they are equal under filters #348, #590, and #986. If the light period is longest the amount of fruiting gradually decreases until none occurs in continuous light except in red-yellow light. This is in general agreement with what occurs in other forms according to Brefeld (1, 2, 3, 4), Klein (12), Schmitz (17), Lendner (13), and Buller (5). Hall (10) has found that no fruiting occurred in *Sclerotinia* under continuous light. The conclusion to be drawn is that too much light is inhibitive to fruiting, and that equal periods of light and darkness are most stimulative. Fruiting can occur, however, in continuous darkness.

The effect of different wave lengths of light on fruiting is very in-

teresting. It seems from this work to show that red light (wave length from  $680\mu$  and longer) is slightly inhibitive to fruiting. Thus fruiting occurs in increasing quantity as the dark period increases to equal that of the light period. If the dark period becomes longer than the light period, the amount of fruiting will fall off, showing that too much darkness is either inhibitive or non-conducive to fruiting. Red-yellow light of wave lengths from 608 to  $571\mu$  is stimulative to fruiting, since a great many sporangia are formed in all series up to those in which the dark periods become longer than the light periods. This shows again that too much darkness is either inhibitive or non-conducive to fruiting. Wave lengths shorter than  $571\mu$  become more and more inhibitive as the violet end of the spectrum is used. Hedgcock (11) discovered this same effect in *Mucor* and *Penicillium*. Even under these wave lengths, an abundance of fruiting will occur if the dark period is long enough for the fungus to overcome the inhibitive effect of the light.

#### ACKNOWLEDGMENTS

The writer wishes to express his sincere gratitude for valuable technical advice given by Dr. J. N. Couch and Dr. J. E. Adams during this work, and for the interest shown by Dr. W. C. Coker, under whose supervision this work has been done.

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## EXPLANATION OF PLATES

## PLATE 36

Graph showing relative number of conidiophores and sporangiophores under each filter in all series. (Small number in upper right hand of each column indicates number of experiments in each series.)

## PLATE 37

- Fig. 1. Petri dish with culture of *Choanephora cucurbitarum*. Upper half of culture exposed to ultra-violet irradiation for 5 minutes.  $\times \frac{1}{2}$ .  
 Fig. 2. Same as above except upper half exposed for 10 minutes.  $\times \frac{1}{2}$ .  
 Fig. 3. Same as above except upper half exposed for 15 minutes.  $\times \frac{1}{2}$ .  
 Fig. 4. Same as above except upper half exposed for 25 minutes.  $\times \frac{1}{2}$ .

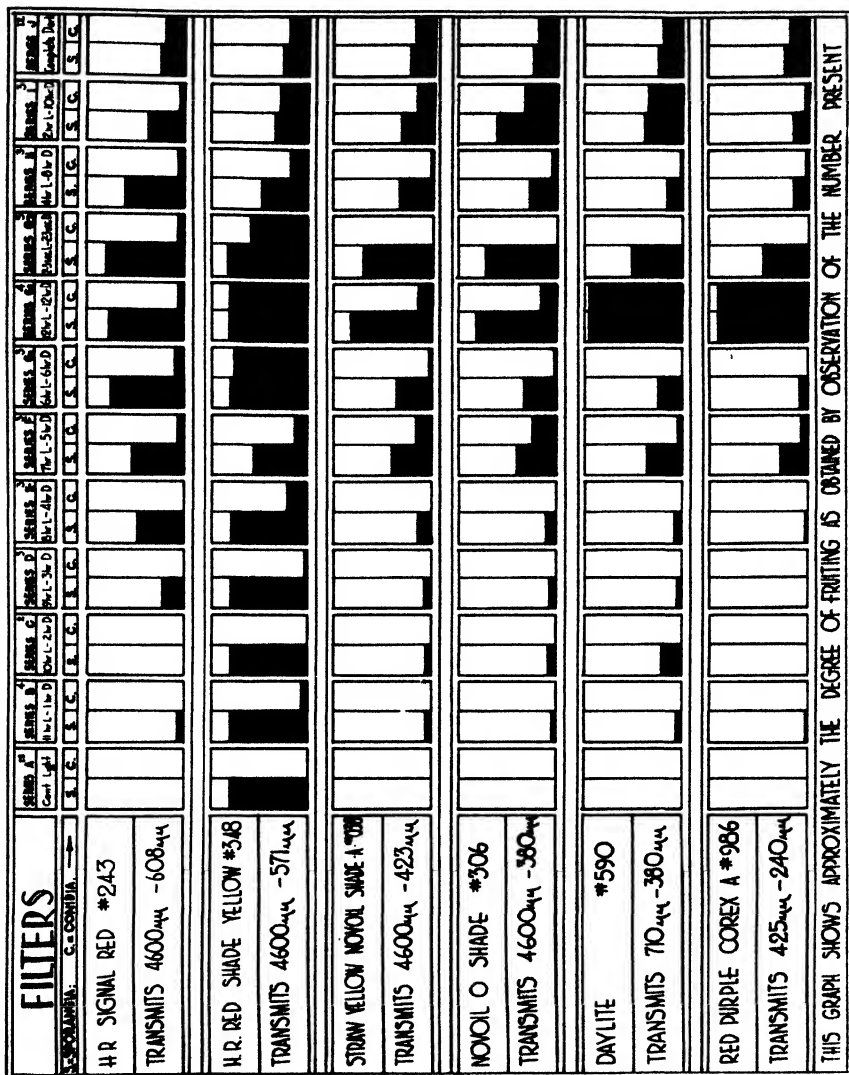
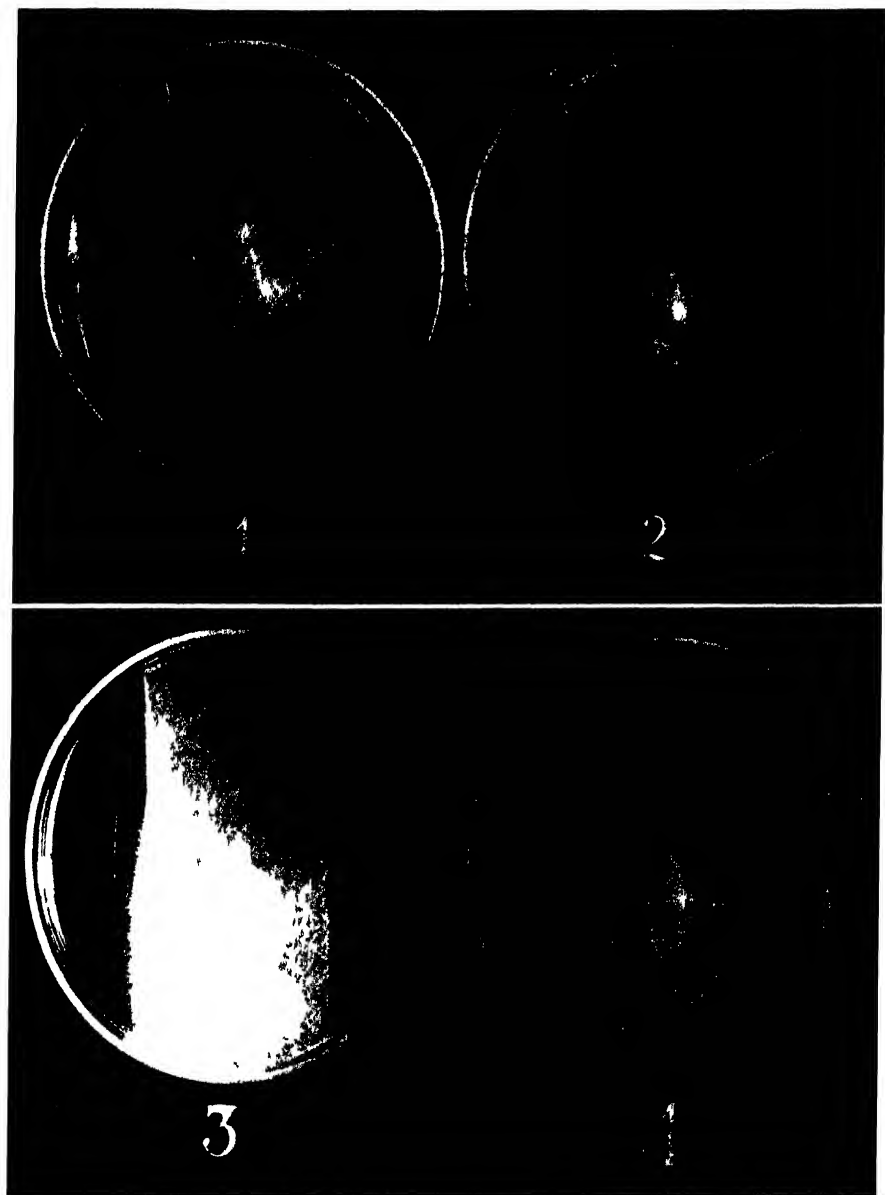




PLATE 37





## NEW SPECIES OF ACHLYA AND APODACHLYA

By W. C. COKER and JANE LEITNER

### PLATES 38 AND 39

The two new species here described were found among many other known water molds by the junior author in her work as a graduate student at the University of North Carolina. The senior author is responsible for drawing up the descriptions and for naming the plants. The drawings are by the junior author.

*Achlya regularis* n. sp.

### Plate 38

Mycelial growth moderately dense, 2.5 cm. in diameter on hemp seed. Hyphae 1-1.2 cm. long, 28-175 $\mu$  thick at base, moderately branching, tapering at the tip. Sporangia plentiful on hemp seed, long-cylindrical, 30-195 x 82.5-442.5 $\mu$ . Spores discharged as in the genus, 10-11 $\mu$  thick. Gemmae plentiful in old cultures, formed by the segmentation of old hyphae into long rows of short, compact, regular cylinders becoming shorter near the base. Oogonia spherical to somewhat obovate with the basal wall bulging inward, 38.5-135 x 90-157.5 $\mu$ , abortive oogonia spherical to sub-spherical, 1-30, mostly 4-10, in an oogonium, rarely oval, excentric when mature, many aborting, 14-59.5 $\mu$  in diameter, mostly 24-28 $\mu$ . Antheridia diclinous, on all oogonia when a strong male strain is present, several applied over the oogonial wall for some distance. Persistently heterothallic, but with weak homothallic tendencies.

Collected from Chapin Lake, one of the fresh-water lakes just inland from the beach at Myrtle Beach, S. C., September 27, 1936. The description was drawn from single-spore cultures on house flies in distilled water which had been filtered through animal charcoal.

*Achlya regularis* belongs to the *bisexualis-imperfecta-flagellata-Klebsiana* group. It is nearest the former, from which it differs in the larger oogonia, more numerous, more variable or often larger eggs, and most obviously in the slender, regular, cylindrical gemmae. The heterothallism, while striking, is not so firmly established.



## NOTES ON CULTURES

The original culture showed abundant oogonia and antheridia, but since the latter were strictly diclinous and the fungus appeared to differ in structure from *Achlya bisexualis* (see Coker, 1927), it was suspected that a second heterothallic species of *Achlya* had been collected.

To determine the sexual responses of the fungus the following experiments have been carried out. Five threads which were giving rise to antheridia were cut out and each planted on a plate of maltose-peptone agar #5. These were designated as males *b*, *c*, *d*, and *e*. Three threads bearing oogonia were isolated but only one, designated as female *c*, survived. Single spore cultures were then made of each of the above strains and cultures have been made from these for all experiments.

The strains of *Achlya regularis*, when kept isolated from strains of the opposite sex, never fruited on hemp seed except on very old cultures. Of these old cultures female *c* and males *c* and *d* were the only ones to fruit, and mites were noticed among the hyphae. The only medium other than the hemp seed on which the strains fruited when grown alone was flies.

On a fly, female *c* produced oogonia and also diclinous antheridia all around the fly, and male *c* produced oogonia and diclinous antheridia in a patch near the head of the fly. The four other male strains produced no oogonia on this or any other medium.

Although the *Achlya* was producing abundant oogonia and antheridia in the original culture on hemp seed, the above mentioned five strains failed to fruit in the first cultures on hemp seed which were put in contact. However, to one of these crosses on hemp seed a house fly was added and in a few days abundant oogonia were observed. This suggested the use of flies and termites as culture media. These were preserved in 70% alcohol and washed before being used. Cultures of the strains of opposite sex were grown on flies and crossed. Later the strains on termites were crossed; and finally the female strain on flies was crossed with the male strain on termites. All of the above crosses were made again but in each case using media which had been autoclaved.

In such crosses on flies and termites oogonia were borne as a rule on a narrow zone between the two strains as in *Achlya bisexualis* and *Dictyuchus monosporus* (Raper, 1936, and Couch, 1926). Sometimes, however, the oogonia were not formed in a line between the two strains

but were scattered over the entire female culture, or in other crosses the oogonia were formed only on the male strain, or in still other crosses the oogonia were scattered irregularly around both strains.

In most crosses there were usually as many spherical oogonia as obovate ones, but in all crosses on termites the oogonia tended to be largely obovate with few spherical ones.

***Apodachlya minima* n. sp.**

Plate 39

Mycelium flaccid and flocculent, reaching a diameter of 2.5–3 cm. on hemp seed; main hyphae slender and segmented, branching from any point on the segment, mainly from the middle; protoplasm thin except in the oogonial branches, with small round refractive bodies present; segments 3.4–8.5 x 47.6–170 $\mu$  on hemp seed, but 6–12.2 x 44–250 $\mu$  on 2% corn meal agar, becoming shorter at the tips. Sporangia unknown (see below for various experiments to produce them). Oogonia numerous, borne on the tips of short, moniliform, often recurved, lateral branches, mainly spherical, occasionally short-pyriform or oval or club-shaped or dumbbell-shaped, 12–16 $\mu$  thick; wall unpitted, smooth, about 0.45 $\mu$  thick. Egg single, completely filling the oogonium, ex-centric, the cytoplasm rounded up into a hyaline ball closely appressed to the smaller hyaline oil droplet. Antheridium originating from the sub-oogonial cell as a lateral branch which grows out and applies itself to the oogonial wall, variable in shape, usually becoming completely empty before the maturation of the egg.

Collected in a branch slightly contaminated with sewage, near the south side of Kenan Stadium, Chapel Hill, N. C., October 21, 1936. The description was drawn from a single-spore culture on boiled hemp seed in distilled water which was filtered through animal charcoal.

Compared with the two (\*) other known species of *Apodachlya*, *A.*

\* Von Minden's species *A. punctata* (1915, p. 586), based only on apparent punctuations in the egg membrane, cannot be accepted without further study. Apinis agrees with Coker that this punctation is only an optical illusion due to the arrangement of minute fat droplets. In our new species of *Apodachlya*, where the mature oogonia have the same appearance as shown by von Minden, we tested this matter as follows: Mature oogonia were treated with chloriodide of zinc, osmic acid and also 95% alcohol, both when with contents and when contents had been squeezed out. All tests indicated that the punctate appearance was due to the fat drops and not to pits in the egg membrane. It must be noted here that if von Minden illustrated a mature oogonium, it would seem to be a new species, but not one based on the character he gives. *Apodachlya seriata* (Lund, 1934) is also poorly founded, so far as described, based only on the larger sporangia in a series up to 4. In *A. brachynema* var. *major* Tiesenhausen (1912) mentions sporangia up to 6.

*pyrifer* and *A. brachynema*, *A. minima* is easily separated by its much smaller oogonia and eggs, by the peculiar origin of the antheridia, and by the persistent refusal to form sporangia under normal or varied cultural conditions.

The origin of the antheridia as short lateral outgrowths in *A. minima* is entirely unlike their direct formation from the sub-oogonial cell in *A. brachynema*. Several of Zopf's figures of *A. pyrifer* show a somewhat similar origin of antheridia as short side branches, but in these cases the oogonia are sessile or nearly so on the sides of long segments.

No one has added important facts regarding the structure of *A. pyrifer* since its original description of Zopf (1884). Seven figures and photographs referred to this species have indeed been published by Cejp (1932), but these add little or nothing to Zopf's treatment. Thaxter mentions its occurrence in America, but did not find the oogonia. The work of Petersen (1910) and Lund (1934) show *A. pyrifer* to be common in Denmark. The former saw the oogonia only once and did not describe them, while Lund does not mention them in *pyrifer* or describe them in var. *macrosporangia*.

#### GERMINATION OF THE EGG

Egg germination in *Apodachlya brachynema* has been observed (Kevorkian, 1935) but not fully described. Egg germination in *Apodachlya minima* occurs in cultures at room temperature about three weeks after mature oogonia are formed. These cultures were not washed, nor was fresh water added, since the addition of water seems to retard germination.

At maturity the egg completely fills the oogonium and contains two hyaline droplets (Pl. 39, Fig. 8), the larger one the cytoplasm and the smaller one the oil droplet. Peculiarly the cytoplasm is hyaline and non-granular, a condition which resembles closely that of the chytrids. At a magnification x 2500 with an apochromatic oil immersion objective the oil and the cytoplasm are indistinguishable in appearance. With an apochromatic immersion objective and at a magnification x 1860 the cytoplasm appears whitish and can be distinguished from the oil which appears greenish. Around the droplets is the single egg membrane which lines the oogonial wall. Germination is initiated in the egg by the cytoplasm's becoming irregular in outline where it is pressed against the oil droplet and a few patches of small granules appearing in the otherwise hyaline cytoplasm (Pl. 39, Figs. 18, 19). The granules become more numerous and the cytoplasm soon loses its spherical

outline. Soon the cytoplasm becomes granular throughout and now occupies all the space inside the wall not filled by the oil droplet (Pl. 39, Fig. 11). The egg enlarges and the pressure that it exerts against the thickened oogonial wall is so great that the wall becomes cracked open, often into two halves. One or two germ tubes are then formed. These are densely filled with cytoplasm and are often club-shaped before the first constriction is formed. The Brownian motion of the granules is rapid and the cytoplasm with many granules flows along the wall of the germ tubes (Pl. 39, Fig. 12). The diminished oil droplet becomes quite small and is finally completely used up. With the growth of the germ tubes the egg becomes completely empty, or nearly so. One of the hyaline plugs of a hypha prevents the back flow of cytoplasm into the old egg by plugging up the constriction nearest the egg. After cracking open the oogonium, the egg often slips out of the old oogonial membrane (Pl. 39, Fig. 13), and falls to the bottom of the dish.

#### EXPERIMENTS TO INDUCE FORMATION OF SPORANGIA

Various media were used in an attempt to bring about the formation of sporangia. The hyphae were grown on hemp seed, termites, house flies, maltose-peptone agar #5, beef extract agar, maltose-peptone agar with 10 gr. peptone, maltose-peptone agar with 10 gr. levulose, maltose-peptone agar with 10 gr. dextrose, and beef extract agar with 10 gr. dextrose.

Cultures were grown in a 1:100,000 eosin solution and in a 1:100,000 hemaglobin solution. These solutions were left in the cultures for three days and then poured off. Distilled water which had been filtered through animal charcoal and autoclaved was poured on the cultures, but the solutions had no effect on them.

Solutions of  $\frac{N}{25}$   $H_3PO_4$  and  $\frac{N}{10}$   $NaOH$  were both used in dilute strength to induce the formation of sporangia. Cultures in the base solutions produced oogonia readily, but cultures in acid solutions produced few oogonia, some having none. The stronger acid solutions caused swelling and bursting of the hyphal tips so that protoplasm exuded from the hypha. No sporangia were formed.

Cultures were also grown in solutions of beef extract, maltose-peptone, maltose-peptone-dextrose, sewage water, and branch water without results.

Cultures on hemp seed, mushroom grubs, in maltose-peptone solu-

tions, double-distilled water, and dilute  $\frac{N}{25}$   $H_3PO_4$  were grown for two weeks in a cold room at 10°C. Only the late production of oogonia was noticed.

Cultures grown on hemp seed, flies, and termites were put in cold chambers at temperatures of 3°C, 7°C, 10°C, 20°C. These cultures were left for three days and then taken into a room at 20°C, but only oogonia were formed.

Cultures on hemp seed were transferred to maltose-peptone solutions at 48°C. After two days the cultures were dead.

Germinating eggs were grown at various temperatures to produce sporangia, but without results.

#### SUMMARY

1. A new species of *Achlya* is described and called *Achlya regularis* because of the regularity of the gemmae. It is primarily heterothallic but with a weak homothallic tendency when grown in certain media.

2. A new species of *Apodachlya* is described and named *Apodachlya minima* because of the small size of its oogonia and eggs. It is compared with all other known species.

3. Numerous experiments were made with different media and change of temperature to induce the formation of sporangia in *A. minima* but without success.

4. Egg germination in *A. minima* was observed. The oogonial wall is cracked open by the pressure of the enlarging egg and the egg often becomes free from the old oogonial shell. Germination is by means of one or more germ tubes.

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## EXPLANATION OF PLATES

### PLATE 38

#### *Achlya regularis*

- Fig. 1. Habit sketch.  $\times 60$ .  
Fig. 2. Sporangium.  $\times 76$ .  
Fig. 3. Gemmae from young culture.  $\times 24$ .  
Fig. 4. Gemmae from old culture.  $\times 24$ .  
Fig. 5. Gemmae at hyphal tip, young culture.  $\times 30$ .  
Fig. 6. Oogonium with one egg.  $\times 265$ .  
Fig. 7. Oogonium with concave basal wall.  $\times 265$ .  
Fig. 8. Oogonium with extreme concave basal wall.  $\times 265$ .  
Fig. 9. Abortive oogonium with antheridium attached.  $\times 265$ .  
Fig. 10. Abortive oogonium.  $\times 130$ .

### PLATE 39

#### *Apodachlya minima*

- Fig. 1. Diagrammatic habit sketch of hypha and oogonia.  
Fig. 2. Young oogonial branch.  
Fig. 3. Oogonium before formation of antheridium.  
Fig. 4. Oogonium with young antheridium.  
Fig. 5. Oogonium with antheridium applied. A wall formed at attachment of oogonium to hypha.  
Fig. 6. Oogonium dumbbell-shaped.  
Fig. 7. Oogonium with egg cytoplasm condensed and hyaline globules formed.  
Fig. 8. Mature oogonium.  
Fig. 9. Oogonium showing oogonial and egg walls. (Walls cross-hatched.)

Fig. 10. Mature oogonium in moniliform formation, observed in a few old cultures.

Fig. 11. Egg showing granular cytoplasm.

Fig. 12. Germinated egg with two germ tubes; the bursted oogonial walls at the side.

Fig. 13. Empty oogonial shell.

Fig. 14. Antheridium androgynous.

Fig. 15. Antheridium diclinous.

Fig. 16. Oval oogonium.

Fig. 17. Pyriform oogonium.

Fig. 18. Club-shaped oogonium.

Fig. 19. Oogonial form rarely seen.

Fig. 1  $\times$  130; fig. 9  $\times$  1862; all others  $\times$  836

PLATE 38

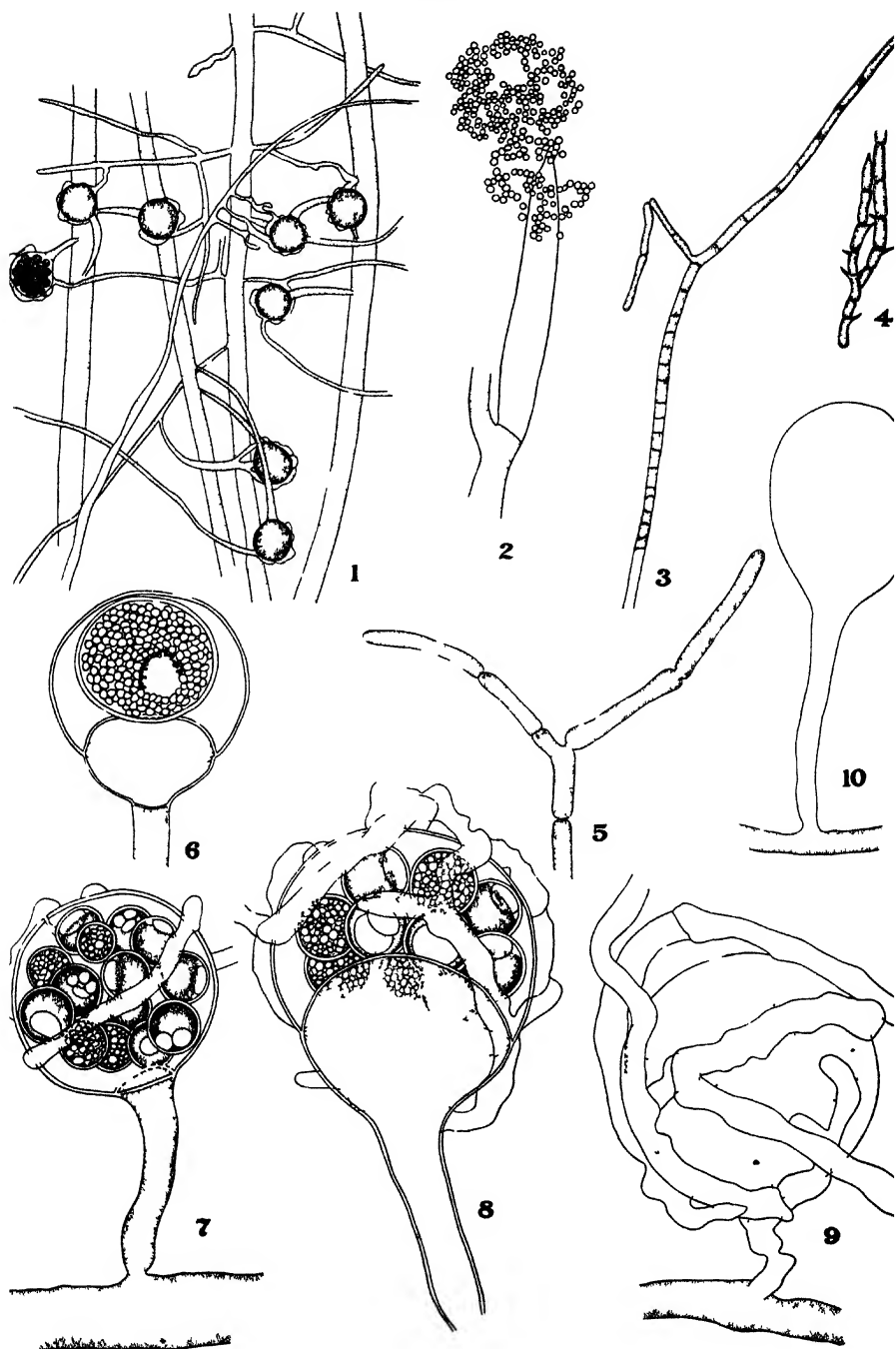
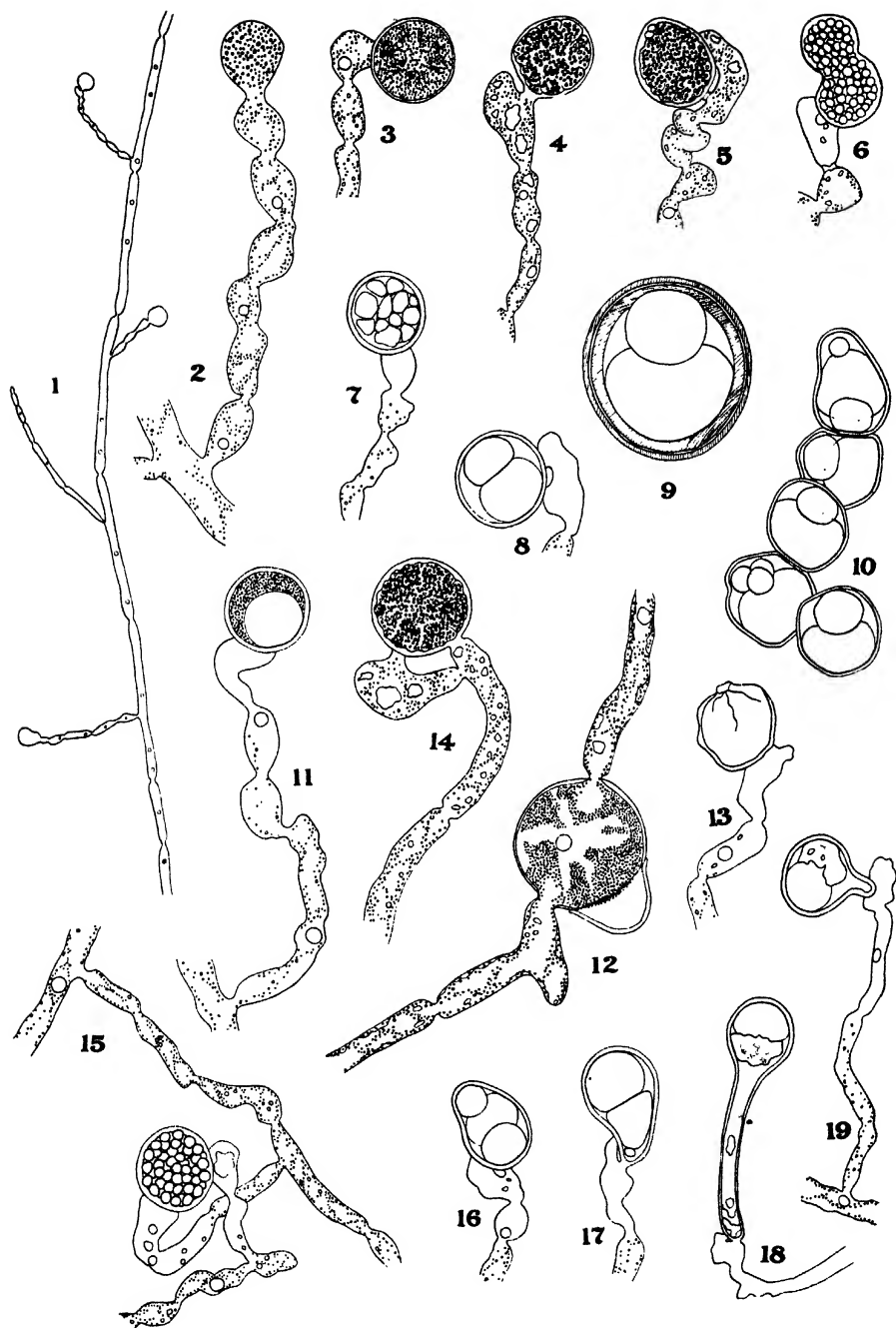






PLATE 39





## A PARTIAL BIBLIOGRAPHY OF NORTH CAROLINA ZOOLOGY

By C. S. BRIMLEY

This is a compilation of papers dealing with the zoology of North Carolina. The titles are from a card catalog which I have kept up for a number of years. Some books are also included where their inclusion would seem to make the paper more useful. The list is necessarily incomplete, but will probably be useful to many.

Most of the papers have been taken from the following periodicals, the names of which have been more or less abbreviated, but by referring to the list the full name can be made out.

American Museum Novitates  
American Naturalist  
American Midland Naturalist  
Annals of the Entomological Society of America  
American Journal of Science  
Auk  
Bird Lore  
Bulletin American Museum of Natural History  
Bulletin Brooklyn Entomological Society  
Bulletin United States Bureau of Fisheries  
Bulletin United States National Museum  
Canadian Entomologist  
Charleston Museum Leaflets  
Copeia  
Ecological Monographs  
Entomological News  
Herpetologica  
Insecutor Inscitiae Menstruus  
Journal Cincinnati Society of Natural History  
Journal Economic Entomology  
Journal of the Elisha Mitchell Scientific Society  
Journal of Mammalogy  
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NORTH CAROLINA DEPT. OF AGRICULTURE,  
RALEIGH, N. C.

## ADVANTAGES OF NORTH CAROLINA RAINFALL

By LEE A. DENSON

In speaking of rainfall, snow and other forms of precipitation will be included, as the records are based on the total amount of water falling to the ground.

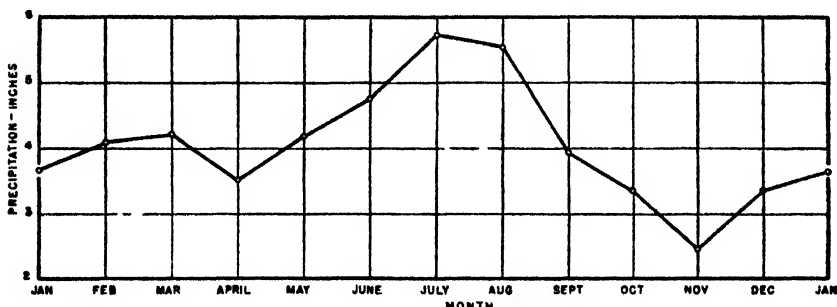
North Carolina forms part of the boundary line of the area of heavier rainfall that extends from the Gulf northward. There are some records running back 75 years or more, but beginning with the general system inaugurated by the Climatological Service of the Weather Bureau in 1887 and continuing through a period of 50 years the state has an average annual rainfall of nearly 50 inches, or to be exact 49.85 inches at the close of 1937. This is about 8 inches more than in Virginia or New England, 7 more than in Pennsylvania or West Virginia, 10 more than in New York or Indiana, and about the same as in Tennessee and Georgia. Less rainfall in the northeastern states, however, is offset in part by a larger number of days with rain or snow, and more extended periods of snow and ice on the ground.

The number of stations in this state has increased from 30 in 1887 to about 120 at this time (1938), and while the value of the record has greatly increased there is still need for more stations, especially on the higher mountain ranges and peaks. The Tennessee Valley Authority has recently established a considerable number of stations at elevations of 4,000 to 6,000 feet that will add much to the value of the mountain records.

In the average annual distribution, beginning at a line in the upper piedmont near Statesville at about 50 inches there is an increase westward to between 55 and 60 inches on the northern Blue Ridge and beyond in Avery County to the Tennessee line, and to 60 or 70 inches or more in the southern Blue Ridge and beyond to Clay County and eastern Cherokee, while the 55-inch area reaches to the Tennessee line of Cherokee, Graham and Swain. Over a limited area on the southern slope there are long records showing 81.18 inches at Highlands and 82.42 at Rock House, Macon County, which are heavier than in any other part of the country except on the North Pacific coast. But there is a sharp decline to about 40 inches in the closed-in valleys of

the cross ranges between the Blue Ridge and the Great Smoky mountains, as in the lower French Broad, and other parts of the section from northern Jackson County to the western part of Yancey. The moisture-laden winds from the Gulf and South Atlantic coasts are uplifted, cooled, and have their moisture condensed and partially exhausted in passing over the mountain heights. They then descend to less elevated and rather inclosed areas, such as the lower French Broad, in comparatively dry form. Part of the rainfall, however, especially in the summer months, comes from local showers and thunderstorms due to local influences and are only indirectly connected with the mass movement of air over the mountain region.

In most of the piedmont and part of the coastal plain the rainfall varies from slightly under 45 to about 50 inches, while in that part of the lower coast section from Pamlico Sound, Carteret and Onslow counties northward to the western end of Albemarle Sound there is an increase to between 50 and 55 inches with a small area near New Bern of 56 inches.



Of course rainfall or water supply is essential to the life and progress of any state or country, and in North Carolina many of the industrial and agricultural activities depend largely upon the ample supply. The outstanding advantages are:

1. The abundant rainfall.
2. The heavier amounts in the mountains, feeding the streams, and forests that conserve the moisture, in flow to the sea, and furnishing a wealth of water power and supply for hydro-electric plants.
3. The graph on monthly averages is interesting in that it would seem that nature is assisting in the distribution, especially in the growing season and the harvesting season. By referring to this graph you will see that the rainfall increases as winter comes on,

and that there is a pick-up in ground supply in the dormant season until March. Then there is a drop of  $\frac{1}{4}$  of an inch in April or planting time when less rain is needed. From May to July there is an increase through the period of cultivation and July and August have the greatest amounts during development and maturity of crops, finally followed by a decline through autumn when dry periods are needed for harvesting.

4. There is no state in the Union having such a long eastern slope to the sea from such high elevations. There are few states with such topography and abundant rainfall combined.

These advantages of water supply and power together with a mean annual temperature of 59° and ample sunshine are strong factors in the building of a great state.

UNITED STATES WEATHER BUREAU,  
RALEIGH, N. C.

## FILMY FERNS IN SOUTH CAROLINA\*

By MARY S. TAYLOR

PLATE 40, FIGS. 1-4

In March, 1935, while collecting liverworts in a deep ravine in Pickens County, South Carolina, the writer's attention was attracted to a huge rock, the vertical face of which was covered with a beautiful vegetative growth, which gave the rock a silvery-green appearance. The rock was completely and densely covered with the delicate, pendulous, closely over-lapping lace-like leaves. The plant resembled a moss but, on examination, proved to be a very delicate little fern. The ravine was dark and the fern was not examined carefully. A few leaves were placed in a packet with liverworts. Many months later, while making a careful examination of the liverworts, the writer came across the dried fern. At first it was thought the fern might be a species of *Trichomanes*. Among the dried material was one leaf with several sori. The sori were borne on a filiform receptacle within a bivalvular, marginal indusium. In all the species of *Trichomanes* known to occur in the United States and familiar to the writer, the indusia are tubular or funnellform. An illustration of a species of *Hymenophyllum* in Douglas Houghton Campbell's "Mosses and Ferns," and a description of the bivalvular indusium, convinced the writer that the fern was a species of *Hymenophyllum*, a genus not previously reported from the North American continent.

The fern was sent to Dr. Wm. R. Maxon, of the Smithsonian Institution, for identification. Dr. Maxon wrote: "It is *H. tunbridgense* (L.) J. E. Smith, a variable species of Great Britain, western Europe, the Azores, Madeira, and the Canary Islands, and in one form or another has been attributed to South Africa, Australasia, Samoa, and tropical America. Some of these forms are now regarded as distinct species, but your plant agrees rather closely with the typical form occurring in Great Britain. My associate, Mr. C. V. Morton, who has given a good deal of attention to *Hymenophyllum*, concurs in the identification."

\* Papers from the Department of Botany, The Ohio State University, No. 408.

The leaves in the South Carolina material average about two inches in length. Many of the leaves are not much over an inch in length, but a number of leaves have been collected that measure three inches in length. Under the lens the beauty and delicate texture of the leaves are revealed. The lamina, or winged expansion, is pale green or olive green, pellucid, and composed of a single layer of cells, making a decided contrast with the thick, dark brown veins. The petioles are very slender and dark brown and are frequently nearly as long as the blades. The rachis is narrowly winged. The pinnae are alternate and pinnatifid, and the margins of the pinnules are distantly and spinulose serrate. The sporangia are sessile and are borne on a filiform receptacle within a bivalvular, marginal indusium, which arises at the tip of a short vein. The sori usually occur solitary at the base of the pinna. The valves, or segments, of the indusium are free, generally to the base, and their upper margins are usually spinulose-dentate. The indusia are at first green, but finally become golden brown in color and are so prominent that they can be easily seen, occurring near the angles formed by the rachis and the mid-veins of the pinnae.

Impressed with the great beauty of the fern-covered rock, the writer and her husband, Bayard R. Taylor, in company with Miss Elise Walker, of Brevard, North Carolina, made many attempts to rediscover the interesting and primitive spot. During the latter part of April, 1937, the same party of three, after many hours of hard walking and climbing, wading cold water, and breaking a way through dense rhododendron, came upon the original station. The rock had lost a little of its pristine beauty, but was still very lovely. The severe blizzard of March, 1936, apparently injured the fern to some extent. After wading cold water, waist-deep, the rocks on the other side of the gorge were examined. The fern was found in dense mats on rocks and on the exposed roots of trees, and also on soil at the base of a rock wall of the gorge. Nine additional stations for the fern were found on this trip, and subsequent exploring trips have increased the number to twenty-one. The writer's records show six other stations, but these need verification. The distribution of the fern, as now known, is limited to a distance of about a mile and a quarter, or possibly a mile and a half. The rock on which the fern was first found by the writer is approximately twenty-two feet long and nearly nine feet high. This rock is completely and densely covered with nearly pure growths of the fern, the creeping, wiry, filiform rhizomes and the very tiny, wiry

roots forming densely interwoven and compact mats. A sample of this rock was sent to Dr. S. Taber, State Geologist of South Carolina, who reported the rock as gneiss, composed of quartz, mica, and feldspar. The fern is not found in abundance at all stations. At some stations the fern is present as small colonies or as scattered leaves, four or five inches apart, but arising from a single rhizome. At other stations it forms compact mats one to two feet in diameter, and in other places occurs in masses two yards square. The fern is found at an elevation of approximately 1,300 to 1,600 feet and grows on rocks that are moist, but not dripping. The air in the part of the gorge where the fern grows is always full of moisture from the spray of the stream as it rushes down from the mountains in a series of beautiful waterfalls. The distribution of the fern appears to be restricted to parts of the gorge which are characterized by the presence of a high degree of humidity, a rather even temperature, and dense shade. On our last trip to these stations on October 9, 1938, Dr. Taylor and I were accompanied by Dr. W. C. Coker of the University of North Carolina.

Material, consisting of specimens from Ireland, Madeira, the Azores, Jamaica, Argentina, Bolivia, and Madagascar, were loaned by Dr. Maxon for comparison. The writer has also examined specimens kindly loaned by Dr. H. A. Gleason, of the New York Botanical Garden. The plant has also been collected in Brazil, Chili, and New Zealand. The plants examined show great variability in respect to size and color of the plants, and the character of the margins of the indusium. The plants from South Carolina agree very closely with the ones collected in Jamaica by Dr. Maxon. Britten (1, p. 16, 17, pl. opp. p. 17, figs. 2, 2a) describes the leaves as one and a half to three inches long, and the upper margins of the valves of the indusium as conspicuously serrate. Heath (2, p. 389, pl. 6, fig. 2) gives the leaves as one to three inches long and sometimes, when very luxuriant, six inches long. Lowe (4, p. 18, pl. 5, fig. B) describes the leaves as one to six inches long and the margins of the indusium as spinulosely serrate. Holloway (3, p. 593, 594, pl. 68, figs. A, B, C, D), in comparing *H. tunbridgensae* and *H. peltatum* Bearne, says that the main distinction between the two species lies in the fact that the margins of the indusium in *H. tunbridgensae* are spinulose-dentate, while in *H. peltatum* they are entire. In the latter species the pinnae are pinnatifid on the upper side only, whence the name "*unilaterale*" by which it was formerly known. He further says that in *H. peltatum* the sori are disposed on the upper side



of the pinnae in a row of two to four, whereas in *H. tunbridgensae* they normally occur singly at the base of the pinna. He says that for the most part these distinguishing features are constantly present, but that he has found undoubted plants of *H. tunbridgensae* showing the pinnae divided unilaterally, and in one instance with the sori in rows. He further says that the margin of the indusium in this species is sometimes only slightly crenulate, while on the other hand the indusial margin in *H. peltatum* is occasionally crenulate instead of being entire.

According to James Britten (1, p. 17) the name *tunbridgensae* commemorates the discovery of the species near Tunbridge Wells, in Kent, England, some years before 1682, in which latter year it was found by Ray in Westmoreland. Britten further states that the species is no longer to be found in the neighborhood of Tunbridge.

The writer now has nineteen stations for *Trichomanes Petersii* A. Gray in the same vicinity. It was found in dense mats on the vertical faces of huge rocks not far from the stream, but is more common on the slightly higher but damp, shaded cliffs. At the present time the *Hymenophyllum* and the *Trichomanes* have not been found on the same rock. The latter has a somewhat wider distribution than the *Hymenophyllum* in the ravine. *Trichomanes Petersii* has been reported heretofore from Tennessee, Georgia, Florida, Alabama, Mississippi, Louisiana, Illinois, and Santo Domingo.

ASHEVILLE, N. C.

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## A FILMY FERN FROM NORTH CAROLINA

By W. C. COKER

PLATE 40, FIGS. 5 AND 6, AND PLATE 41

During last August while scouting in the deep Cullasaja gorge and its tributary gorges, Dr. Herbert Hechenbleikner, who was working with me on the flora of Macon County, N. C., with headquarters at the Sam T. Weyman Memorial Laboratory at Highlands, found for the first time in North Carolina the interesting filmy fern *Trichomanes Boschianum* Sturm. The plant has never before been reported in the Atlantic Coastal states north of Georgia, but through the kindness of Dr. Edgar T. Wherry we can now also add this fern to the flora of South Carolina. He writes us that he has found a specimen of it in the herbarium of the Academy of Natural Sciences of Philadelphia (No. 2096), collected at Tomassee Falls, Oconee County, S. C., on May 5, 1906, by Dr. H. D. House. In the United States except for Florida it has previously been reported only in scattered localities in Alabama, Georgia, Tennessee, Kentucky, Ohio, and West Virginia. The Florida station appears to be lost.

Our plants were found on Crow Creek under the largest falls, not far from U. S. G. S. bench mark #520 and about a quarter of a mile below the high Cullasaja Falls, altitude about 3000 feet. The falls here have a drop of about 35 feet, running over a rock shelf which projects about 20 feet over the cavern below. At the innermost recess where the overhanging shelf meets the floor of the cave, where one must crawl to reach, this strangely exacting fern had found a congenial home.

The discovery by Mrs. Taylor of two other filmy ferns in Pickens County, S. C. (see preceding paper), one of them new to the North American continent, makes three species of this remarkable family for the Carolinas. Before Mrs. Taylor's discoveries, no member of this family, with the exception of the collection by Dr. House mentioned above, had ever been found in these two states.

Dr. Hechenbleikner's notes are as follows:

"This patch of *T. Boschianum* consisted of approximately 100 or 150 fronds, some of which were growing erect while others were hanging

down from the sloping roof formed by the over-hanging cliff. The plants were kept continually moist by seepage from the roof and by occasional spray from the falls. The numerous fronds arose from black rhizomes which were fastened to the shallow substratum by the roots. From the situation of the fern it seemed that at no time during the day did the plants ever receive the direct rays of the sun.

"Since *T. Boschianum* is usually found on a sandstone substratum, a sample of the rock from the cliff was taken and tested for hydrogen ion concentration. The pH of the surface material scraped from the rock (i.e., the rock itself) was 5.45, or distinctly acid. Samples taken from the interior of the rock tested as pH 6.54, thus being less acid than the surface. Both determinations were made with a Beckman pH meter having a standardized calomel cell and capable of accurate results within .02 of a pH. The rock tested was a granitic gneiss.

"Both *Asplenium montanum* and *A. trichomanes* were found along the base of the over-hanging cliff near *T. Boschianum*. The strong draft from the waterfall made it very difficult to get a good photograph of the fern, and several trips were necessary before the accompanying one was secured."

DEPARTMENT OF BOTANY,  
UNIVERSITY OF NORTH CAROLINA,  
CHAPEL HILL, N. C.

#### EXPLANATION OF PLATES 40 AND 41

*Hymenophyllum tunbridgense*, Pickens County, S. C. Fig. 1, habit sketch,  $\times$  slightly over 2, drawn by Mrs. Cecil Johnson; fig. 2, sorus  $\times$  8, drawn by Mrs. Johnson; fig. 3, spores  $\times$  502, by Alma Holland.

*Trichomanes Petersii*, Pickens County, S. C. Fig. 4, habit sketch,  $\times$  1½, drawn by Mrs. H. M. Burlage.

*Trichomanes Boschianum*, Macon County, N. C. Fig. 5, habit sketch, natural size, drawn by Miss Laurie Stewart; fig. 6, sorus  $\times$  9, drawn by Dr. Hechenbleikner.

PLATE 40

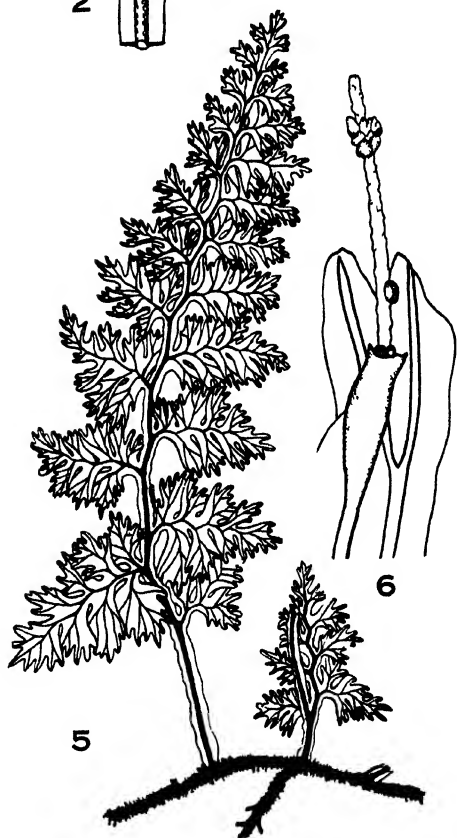
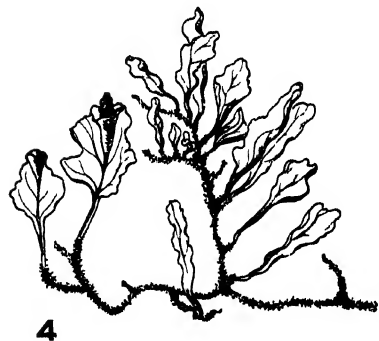
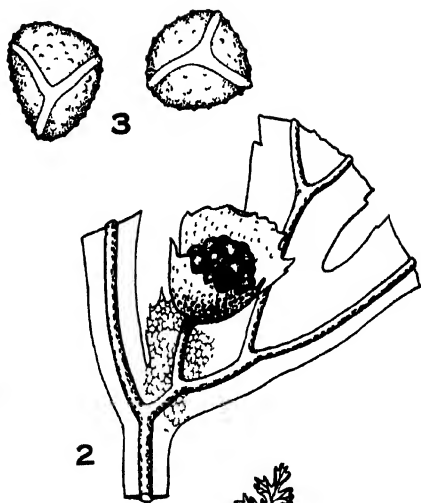
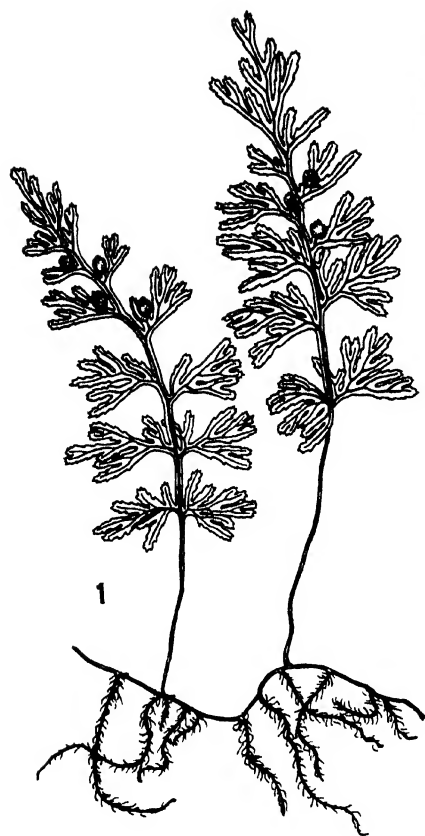




PLATE 41



TRICHOMANES BOSCHIANUM, MACON COUNTY, N. C.



